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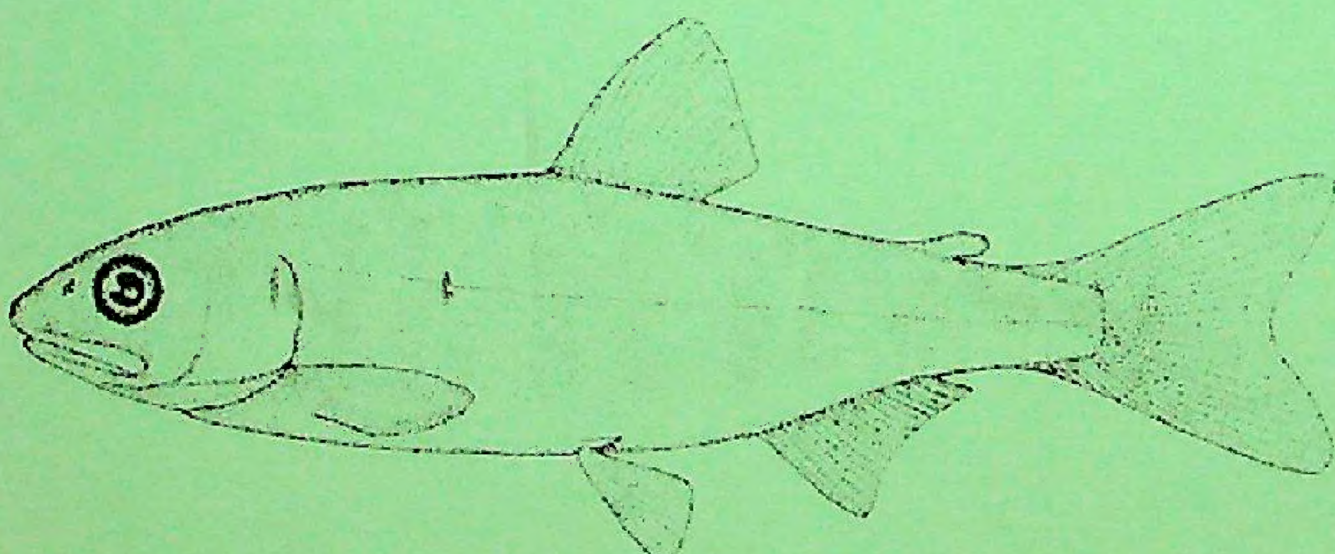

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Drawing by Robert McDowall, from: McDowall, R. 1990. New Zealand freshwater fishes: A natural history and guide. Heinemann-Reed, Auckland, New Zealand. Used with permission of the artist.

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INVERTEBRATE DRIFT AND FEEDING HABITS OF JUVENILE CHINOOK SALMON IN THE UPPER SACRAMENTO RIVER, CALIFORNIA

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The diurnal feeding habits of juvenile chinook salmon, *Oncorhynchus tshawytscha*, rearing in the upper Sacramento River from April to June 1996 were examined in relation to food availability. Daily mean drift densities in the Sacramento River ranged between 211 and 2,100 organisms/100 m^3. Aquatic taxa, especially Chironomidae (Diptera) and Baetidae (Ephemeroptera), dominated drift samples and salmon stomach contents. Selection of prey by juvenile chinook salmon appeared to be based on size, abundance, or conspicuousness of organisms, as indicated by linear selection indices. The gape width of juvenile salmon increased predictably as the fish grew in length, but the sizes of prey consumed fell considerably short of gape potential due to the relative rarity of large prey in the environment. Mean stomach fullness was 2.4% of fish weight, indicating reasonable feeding opportunity during spring of wet years similar to 1996.

INTRODUCTION

Juvenile chinook salmon, *Oncorhynchus tshawytscha*, generally spend from several weeks to several years rearing in freshwater before migrating to the ocean. Most juvenile chinook salmon in the Sacramento River display an ocean-type life history strategy (Healey 1983), emigrating as subyearling fry or smolts. Although the time spent in the upper river can be short, growth in size and stored energy during early rearing can ultimately determine survival to the estuarine or ocean phase (Higgs et al. 1995). Consideration of important features of the environment, such as food availability, along with the response of the fish (e.g., food selection) to those habitat features, allows for a greater understanding of the role of freshwater rearing in the life history of juvenile chinook salmon.

The feeding habits of juvenile chinook salmon in other river systems have been studied extensively (Becker 1970, 1973; Sagar and Glova 1987, 1988; Rondorf et al. 1990). Schaffter et al.[2] (1982) described the drift and diet of juvenile chinook salmon

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[2] Schaffter, R.G., P.A. Jones, and J.G. Karlton. 1982. Sacramento River and tributaries bank protection and erosion control investigation: Evaluation of impacts on fisheries. Final report. California Department of Fish and Game, Red Bluff, California, USA.

in the Sacramento River in 1981, and Merz and Vanicek (1996) did the same for the lower American River, a Sacramento River tributary, in 1992 and 1993; however, recent published studies focusing on food availability and feeding habits of juveniles in the upper mainstem Sacramento River are lacking. Fall-run, late-fall-run, winter-run, and spring-run chinook salmon stocks use the upper Sacramento River and its tributaries for spawning. Numerous anthropogenic changes to the river, such as construction of dams, flow regulation and diversion, stream channelization, conversion of vast areas of floodplain to agriculture, and gravel extraction, among others, have contributed to the decline of all 4 stocks (Brown 1991, Fisher 1994). The listings of the winter run as endangered (NMFS[3] 1994) and the spring run as threatened (NMFS[4] 1999) under the federal Endangered Species Act limit the sacrifice of specimens for diet studies, whereas, ironically, the stocks' imperiled status makes understanding their life history, behavior, and habitat requirements ever more crucial. Given the possibility of future endangered species listings of the other Sacramento River chinook salmon stocks, it is important for conservation purposes to understand the role that environmental factors play in limiting salmon populations. The present study provides insight into seasonal food availability and diet that is applicable to all stocks of salmon in the river, though only fall-run young-of-the-year were sacrificed for stomach analyses.

The main objectives of this study were to describe 1) the availability of natural foods (invertebrate drift) in the upper mainstem of the Sacramento River during April–June 1996, 2) the taxonomic composition of organisms in the diet of juvenile chinook salmon rearing in the upper mainstem river during that time, 3) prey selection by juvenile salmon, 4) size characteristics of prey in the diet of juvenile salmon in relation to fish size, and 5) feeding intensity and energy intake of juvenile salmon.

METHODS

Study Area

Originating near Mt. Shasta in northern California, the Sacramento River extends approximately 595 river km (rkm) along the floor of the Central Valley to its mouth in the Sacramento-San Joaquin Delta. Bordered by the Sierra Nevada and Cascade ranges on the east and the Klamath and Coast ranges on the west, the northern Central Valley is characterized by heavy precipitation during winter and spring and negligible precipitation during summer and fall.

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[3] NMFS (National Marine Fisheries Service). 1994. Endangered and threatened species; status of Sacramento River winter-run chinook salmon. Federal Register 59:440-450.

[4] NMFS (National Marine Fisheries Service). 1999. Endangered and threatened species; threatened status for two chinook salmon evolutionarily significant units (ESUs) in California; final rule. Federal Register 64:50393-50415.

Fed primarily by runoff from precipitation and snowmelt from surrounding mountains, the Sacramento River at Red Bluff historically exhibited flow ranging from about 28 m^3/s in summer to 100-year flood levels of about 11,900 m^3/s (CDWR[5] 1994a). River discharge is now regulated by the Shasta-Keswick Dam complex (rkm 501 and rkm 486), the operation of which tends to dampen oscillation in the hydrograph, as compared to historic flows (CDWR[6] 1994b). River flow in the study area largely depends upon the management of water projects upstream. Major water diversions located in the study area include the Anderson-Cottonwood Irrigation Diversion (rkm 481), the Red Bluff Diversion Dam (RBDD) (rkm 391), and the Glenn-Colusa Irrigation Diversion (rkm 332). The river provides the main water supply for the cities of Redding, Chico, and Red Bluff, in addition to supporting agricultural and recreational water uses.

Study Sites and Duration

We investigated the available foods for juvenile chinook salmon at 5 sites on the upper mainstem Sacramento River between rkm 380 and rkm 430 during April–June 1996 (Table 1, Fig. 1). Feeding habits data from juvenile fall-run chinook salmon were collected at 9 sites between rkm 311 and rkm 444 (Table 1, Fig. 1) during the same period.

Drift Collection and Handling

Field Collections of Invertebrate Drift

Food abundance was estimated by arranging up to 4 replicated drift nets in a transect perpendicular to the river's edge. Sampling was repeated throughout the day at a given site. The drift samples were collected between sunrise and sunset to compare with daytime feeding habits data. Drift was sampled at 1 site per week, not concurrently with fish sampling efforts.

Two types of drift nets were used. The 1st type had a mesh size of 260 µm and mouth dimensions of 45 x 30 cm. These nets could be oriented with either the long or short side parallel to the substrate and were most appropriate for sampling shallow near-shore areas. The second net type had a 75 x 15.5 cm mouth and 64 µm mesh, and was most often used in deeper water farther from shore, where the shorter nets could not capture surface drift. Drift nets sampled the water for 15–25 minutes. After removal of a net from the water, the contents were washed down to the closed end of the net. The sample was sieved to remove excess water and preserved in 10% formalin. Rose bengal dye was added to each sample to facilitate sorting of organisms.

[5] CDWR. 1994a. Sacramento River bank erosion investigation progress report. California Department of Water Resources, Northern District, Red Bluff, California, USA.

[6] CDWR. 1994b. Use of alternative gravel sources for fishery restoration and riparian habitat enhancement in Shasta and Tehama counties, California. California Department of Water Resources, Northern District, Red Bluff, California, USA.

Table 1. Sites and dates of fish and drift collections in the upper Sacramento River, April–June 1996.

Site (rkm)	Fish collection dates	Drift collection dates
444	4/26	not sampled
438	4/12, 5/10, 6/21	not sampled
430	not sampled	4/7, 5/19, 6/30
415	4/12, 4/26	4/14, 6/2
396	4/11, 4/26, 5/9	5/3, 6/23
391	4/20, 5/23	4/20, 5/13, 6/23
390	4/25, 5/23	not sampled
380	4/11, 4/25, 5/9, 5/23, 6/6, 6/20	5/5, 6/9
352	4/11, 4/25, 5/9, 5/23, 6/6, 6/20	not sampled
311	4/11, 4/25, 5/9, 5/23	not sampled

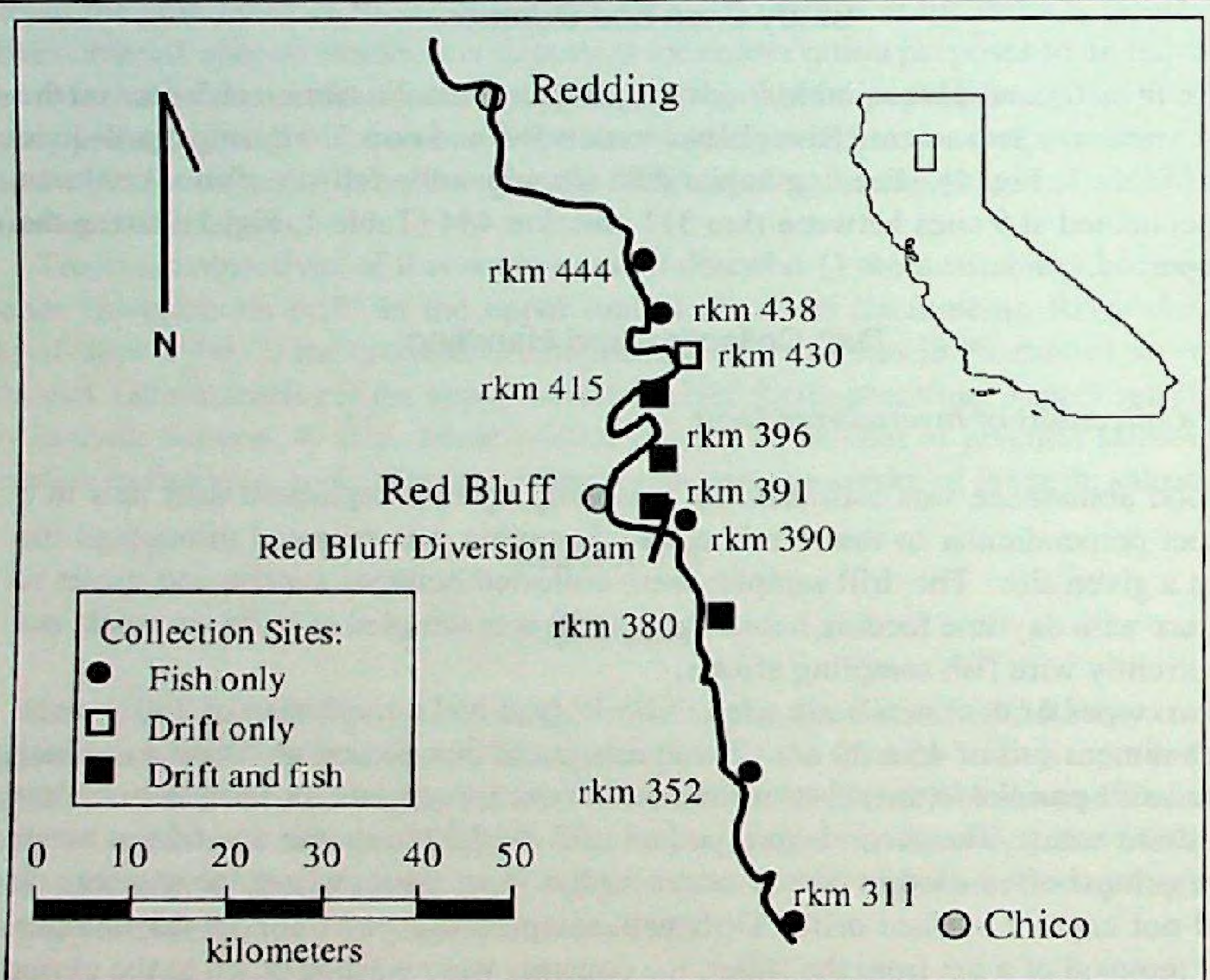

Figure 1. Map of collection sites for invertebrate drift and juvenile chinook salmon in the upper Sacramento River, April–June 1996.

Drift Sample Processing

To expedite processing, some drift samples were suspended in water and divided into subsamples using a Folsom plankton splitter. In order to identify a minimum of 100 organisms per sample, sorting ranged from an entire sample to as little as 1/8 of

a sample. The sample or subsample was viewed under a lighted magnifying lens. Invertebrates and fish larvae were sorted from the sample and transferred to a bottle of 80% ethanol. Sorted organisms were identified using published keys (Usinger 1956, Pennak 1978, Merritt and Cummins 1984, Arnett 1985). Drift density (DD, the number of organisms per 100 m^3 of water) was estimated with the equation:

$$DD = 100 \times (\text{number of organisms per net-hour} / m^3 \text{ filtered per net hour}).$$

The number of organisms per net-hour was calculated after adjusting for subsample size.

Juvenile Salmon Collection and Handling

Fish Collection

Beach seines (1.21 m × 9.09–22.73 m, 3.2-mm stretch mesh) were used to collect juvenile chinook salmon from gravel bar and boat ramp sites. Sites were sampled between 0800 and 1600 hours once every 2 weeks. After capture, juvenile salmon were anesthetized with tricaine methanesulfonate (MS-222), and each individual was assigned to a run (fall, late-fall, winter, or spring) based on fish length and date of capture using a run identification model (Fisher[7] 1992, as modified by Greene[8] 1992). A subsample of up to 10 fall-run salmon per site was sacrificed by prolonged exposure to the anesthetic and preserved in 10% formalin.

Diet Analysis

Juvenile salmon were examined to determine the number, size, taxonomic composition, and total wet weight of organisms in stomach contents. Preserved fish specimens were measured to the nearest millimeter (FL), blotted, and weighed to the nearest milligram. Dial calipers were used to measure the gape width of each fish specimen to the nearest 0.05 mm. The stomach was excised and blotted, and the stomach weight, with and without the contents, was determined to the nearest 0.01 mg. The total wet weight of the contents was calculated by subtraction. The stomach fullness index (SFI) (Hyslop 1980) for each fish was calculated with the equation:

$$SFI\ (\%) = 100 \times (\text{wet weight of stomach contents}) / (\text{fish wet weight}).$$

Stomach contents were viewed under a microscope fitted with an ocular micrometer. Each organism was identified to the lowest practical taxonomic level

[7] Fisher, F.W. 1992. Chinook salmon *Oncorhynchus tshawytscha* growth and occurrence in the Sacramento-San Joaquin River system. California Department of Fish and Game, Inland Fisheries Division, Red Bluff, California, USA.

[8] Greene, S. 1992. Estimated winter-run chinook salmon salvage at the State Water Project and Central Valley Project delta pumping facilities. Memorandum to R. Brown, 5/8/92. California Department of Water Resources, Sacramento, California, USA.

(family in most cases) and its life stage (larva/nymph, pupa, or adult) was recorded when possible. The first 10 representatives encountered from each invertebrate taxon were measured for head capsule width (HCW) to the nearest 0.03 mm, for organisms with a head capsule. Head capsule widths were used to represent relative invertebrate prey size, as fragmentation of prey during swallowing and digestion precluded the use of other measures, such as prey length. Total lengths of fish larvae found in the stomach were measured to the nearest millimeter if the condition of the specimen permitted. Copepods, cladocerans, nematodes, and aquatic worms were counted if present, but were not measured. Fragments of organisms without a head attached (legs, wings, or abdomens) were neither counted nor identified; it was assumed that the source organism had already been represented in the count of heads or head capsules.

Selection of individual taxa by juvenile chinook salmon was calculated from abundance in the drift, totaled across all sites and sampling dates, and compared with the abundance in the diet of all fish examined, using the linear selection index (L) (Strauss 1979). The index is described by the equation:

$$L = r_i - p_i,$$

where r_i is the relative abundance (expressed as a proportion) of taxon i in the diet of chinook salmon and p_i is the proportion of taxon i in the drift during the same time period. The index ranges from +1 to −1, with positive values indicating preference, negative values indicating avoidance or inaccessibility, and zero values indicating random feeding (Strauss 1979).

Statistical Methods

Student's t-tests were used to analyze the null hypothesis that L = 0 for each taxon (Strauss 1979). Taxonomic groups present in low numbers in both the environment and the diet were excluded from the analysis of L. Least squares regression was used to evaluate the relation between fork length and fish gape width or prey head capsule width (HCW) (mean, maximum, and minimum). For fork length-HCW regressions, only fish with >10 items in the stomach were used, to reduce variability due to low feeding intensity and low selection. To normalize the data on number of prey per stomach, the data were square-root transformed for calculation of means and confidence intervals, then reverse transformed for presentation. The significance level was $\alpha = 0.05$.

RESULTS

Drift Density

Daily mean drift density in spring 1996 ranged from 211 to 2,100 organisms/100 m^3 (Table 2) and the overall mean was about 617 organisms/100 m^3. Mean drift density fell below approximately 800 organisms/100 m^3 on most sample dates, but 2 higher

estimates (1,537 and 2,100 organisms/100 m^3) were recorded on 23 June 1996 at rkm 396 and rkm 391 (Table 2). The lowest mean drift densities were estimated for rkm 415 during April and June (211 organisms/100 m^3 for both months). Aside from the 2 high estimates, daily mean drift density showed no distinct spatial patterns (Fig. 2).

Relative Abundances of Drift and Diet Taxa

The drift during April–June 1996 was dominated by aquatic taxa, which made up about 96% of organisms captured (Appendix A). The most prevalent members of the drift were larvae, pupae, and adults of the family Chironomidae (Diptera), which made up 54% of the total number of organisms (Appendix A). The high abundance of chironomids accounted for the high general contribution of the order Diptera. The family Baetidae (Ephemeroptera), particularly nymphs, also were present in large numbers in the drift, with 12% of the total. Taxa contributing 3–6% of the drift included simuliid (Diptera) larvae (4.16%), oligochaetes (5.72%), cladocerans (4.79%), copepods (4.98%), and fish larvae (3.42%, including Catostomidae). Other taxa contributed relatively small numbers to the drift.

The diets of 153 juvenile chinook salmon were examined; among these, no empty stomachs were present. As for the drift, the diet was dominated by aquatic taxa, which made up 94% of consumed items (Appendix A). Chironomids of all life stages were the predominant prey, collectively making up >63% of the diet during April–June 1996. The order Diptera made up about 68% of the diet, mostly due to the high contribution of chironomids. Baetid nymphs and adults were common prey, with a combined 14% of the total. Homopterans (3.30%), trichopterans (3.92%), and fish larvae (3.30%, including catostomids) were also found in notable numbers in salmon stomachs.

Table 2. Mean, standard error (SE), and coefficient of variation (CV%) for drift density (number of organisms per 100 m^3 water filtered per net) by site and date for the upper Sacramento River, April–June 1996.

Site (rkm)	Date	Number of samples	Mean drift density (No./100 m^3) (+/–SE)	CV%
430	4/7/96	6	805 (270)	82
	5/19/96	11	638 (169)	88
	6/30/96	9	295 (54)	55
415	4/14/96	11	211 (34)	54
	6/2/96	10	211 (32)	48
396	5/3/96	2	483 (161)	47
	6/23/96	2	1,537 (291)	27
391	4/20/96	6	484 (107)	54
	5/13/96	14	670 (201)	112
	6/23/96	9	2,100 (1,192)	170
380	5/5/96	15	363 (64)	69
	6/9/96	12	538 (125)	81

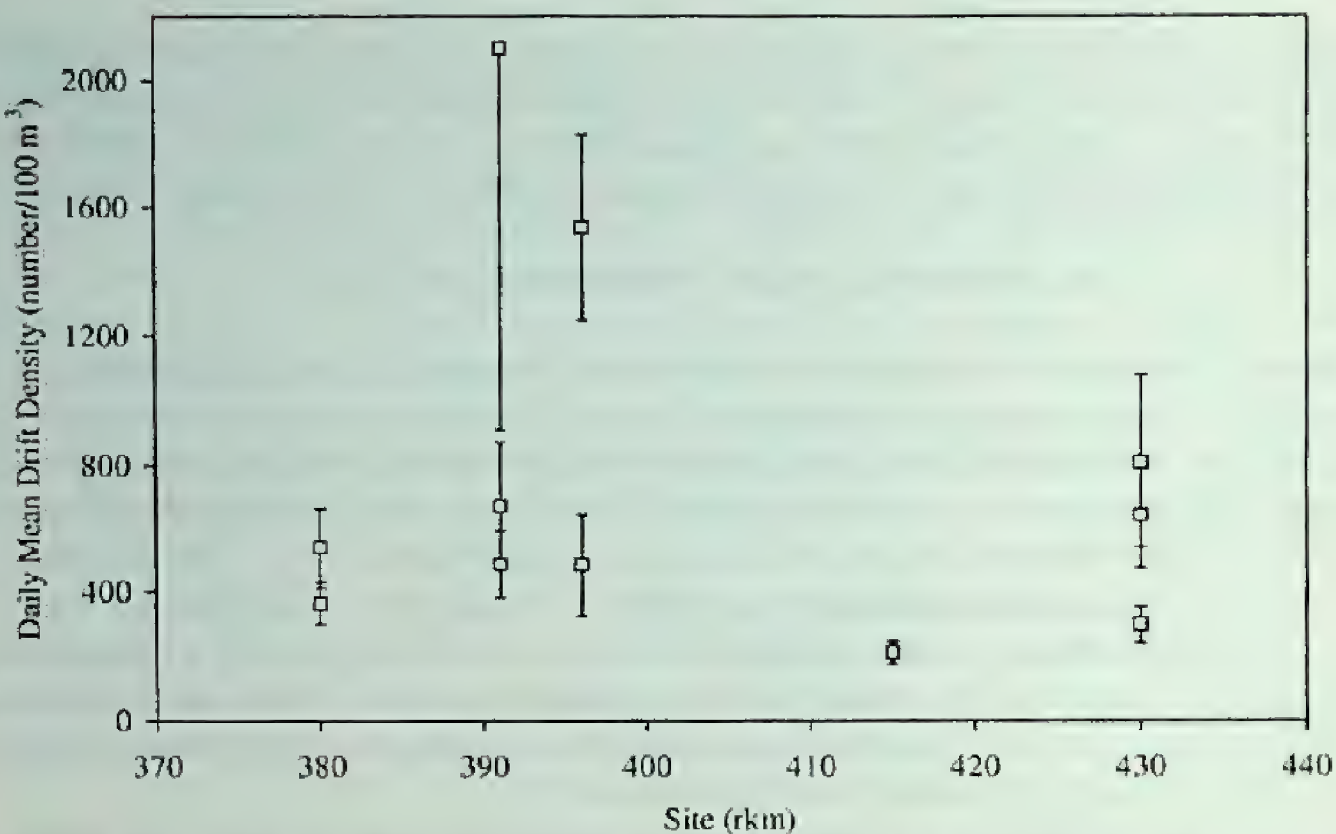

Figure 2. Daily mean drift density (±SE) plotted as a function of site location on the Sacramento River for April–June 1996. The upper SE limit (3,292) for the highest value at rkm 391 was omitted for scaling purposes.

Selection of Available Prey by Juvenile Chinook Salmon

For many groups, the linear selection index was not significantly different from 0, suggesting random selection of those items. Values of L ranged from –0.19 to a maximum of 0.17 (Fig. 3), reflecting the conservative nature of the index, which only approaches extreme values when an item is rare but consumed almost exclusively, or is highly abundant but rarely consumed (Strauss 1979). Among the taxa numerically common in the drift, significant negative values of L were observed for chironomid larvae (–0.19), oligochaetes (–0.06), and cladocerans (–0.05), whereas significant positive values were calculated for chironomid pupae (0.12) and chironomid adults (0.17) (Fig. 3). Collembolans, baetid nymphs, aphid (Homoptera) adults, simuliid larvae, hydropsychid (Trichoptera) larvae, hymenopterans, and water mites (Hydracarina) displayed weak, but significant, selection values (Fig. 3).

Fish Size, Gape Size, and Prey Size Relations

The gape width of juvenile chinook salmon showed a significantly positive linear relation with fork length ($y = 0.0864x - 0.5658$; $r^2 = 0.82$, $n = 153$, $P < 0.0001$) (Fig. 4). The slope of the relation between fork length and head capsule width (HCW) of measurable invertebrate prey was highest for maximum HCW and lowest for minimum HCW (Fig. 4). The amount of variability in HCW explained by fork length also decreased from maximum to mean to minimum HCW. The relation between fork length and maximum HCW was significantly positive ($y = 0.0238x - 0.3109$; $r^2 = 0.32$, $n = 113$, $P < 0.0001$), as was the relation between fork length and mean

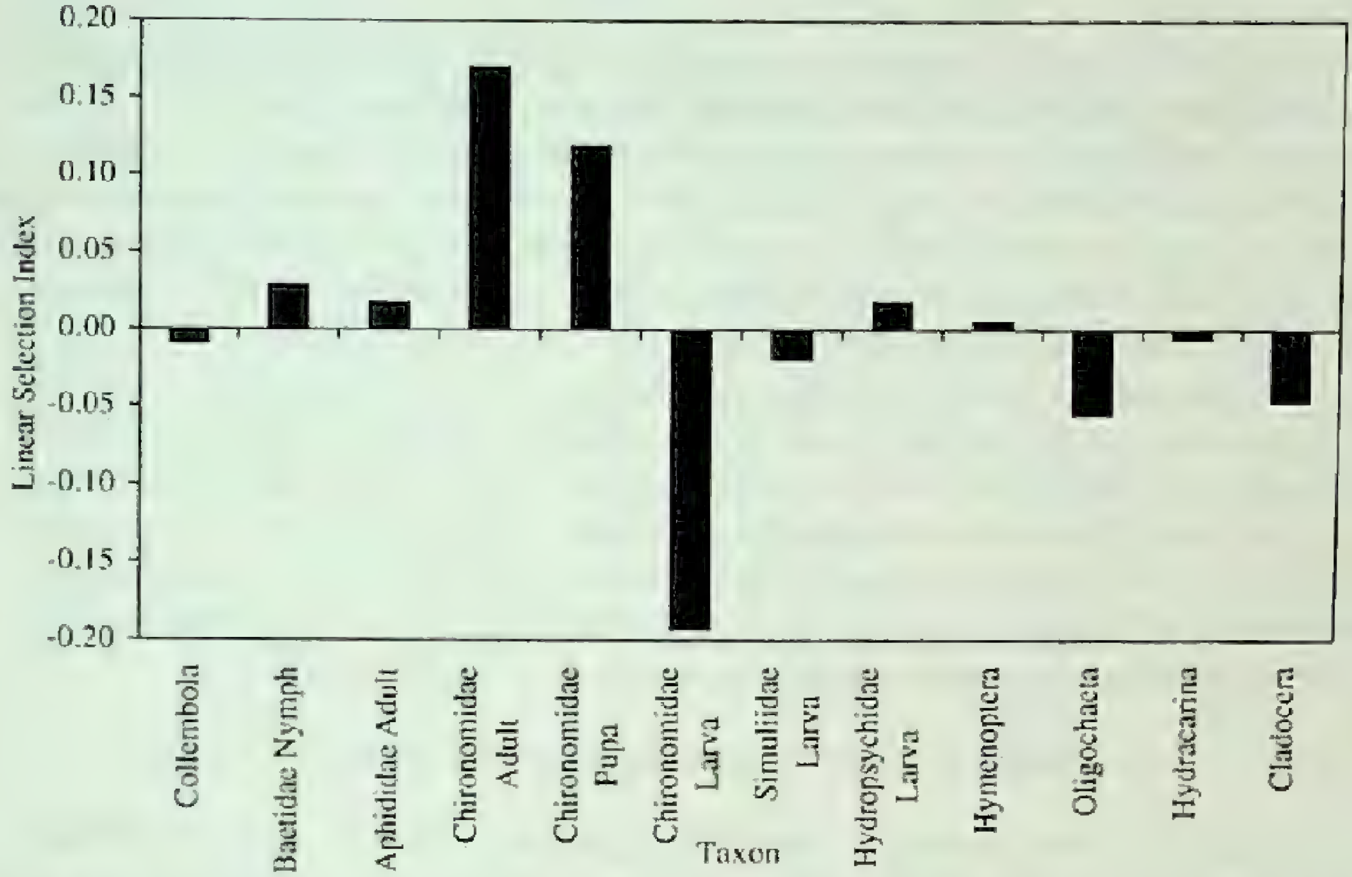

Figure 3. Significant linear selection indices (L) for common taxa in the drift and diet of juvenile chinook salmon in the upper Sacramento River, April–June 1996. Possible values of L range from −1 to 1.

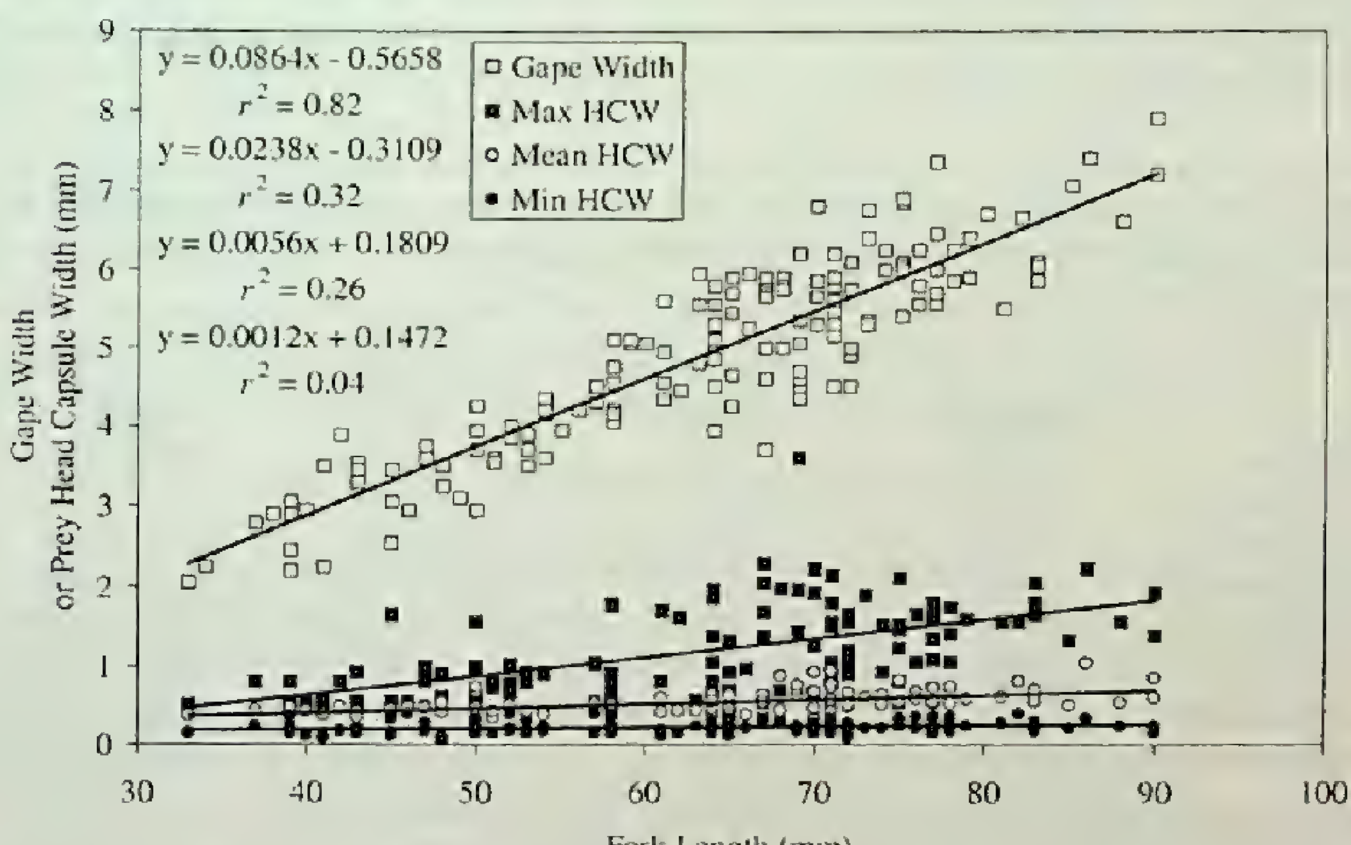

Figure 4. Regressions of gape width (n = 153), and maximum, mean, and minimum head capsule width (n = 113) of invertebrate prey on fork length of juvenile chinook salmon captured April–June 1996 from the upper Sacramento River.

HCW ($y = 0.0056x + 0.1809$; $r^2 = 0.26$, n = 113, P <0.0001). Although the regression of minimum HCW on fork length was significantly different from 0, it explained only 4% of the variability in minimum HCW ($y = 0.0012x + 0.1472$, $r^2 = 0.04$, n = 113, P <0.05). The mean gape width of all fish examined was 4.92 mm (SE = 0.56, range = 2.05–7.90 mm, n = 153). The mean HCW of measurable invertebrate prey items was 0.53 mm (SE = 0.01, range = 0.06–3.60 mm, n = 3,086). Chironomid larvae were the smallest of the common prey items as measured by HCW, whereas hydropsychid larvae were among the largest invertebrate prey (Table 3).

Fish larvae did not make up a large percentage of the total number of items in the diet, and the size of fish prey, measured in length, cannot be compared directly with the sizes (HCW) of invertebrate prey. However, there was a trend in the relation between the size of juvenile chinook salmon and the number of fish larvae consumed. Of the salmon (n = 31) that consumed fish larvae, all were ≥40 mm FL. Only juvenile salmon ≥60 mm FL had stomachs containing ≥5 fish larvae (the maximum was 38). Fish larvae in salmon stomachs ranged from 3 to 18 mm total length.

Feeding Intensity and Stomach Fullness

The number of prey items per stomach and stomach fullness index (SFI) were used as measures of the feeding intensity or energy intake of juvenile chinook salmon in the Sacramento River. Arrangement of mean number of prey items per stomach and the SFI into 3 size classes and 3 monthly categories revealed no clear trends in feeding intensity (Table 4). During April, the highest mean SFI was seen in the smallest size class (30–50 mm). However, in June, both the mean number of prey per stomach and the mean SFI increased with fish size. The SFI averaged about 2.4% (SD = 1.6, n = 153) and ranged from 0.5% to 8.4% of wet weight.

Table 3. Mean, standard deviation (SD), and range of head capsule widths (HCW) of common taxa in stomachs of juvenile chinook salmon captured from the upper Sacramento River, April–June 1996.

Taxon	Life stage	Number measured	Mean HCW (+/–SD)	Range
Baetidae	Adult	29	0.84 (0.10)	0.63–1.05
Baetidae	Nymph	325	0.74 (0.17)	0.24–1.11
Aphididae	Adult	103	0.42 (0.06)	0.27–0.60
Chironomidae	Adult	817	0.45 (0.08)	0.15–0.84
Chironomidae	Pupa	501	0.47 (0.08)	0.21–0.87
Chironomidae	Larva	585	0.27 (0.09)	0.09–0.63
Simuliidae	Larva	105	0.44 (0.11)	0.18–0.75
Hydropsychidae	Larva	118	1.13 (0.36)	0.39–2.22

Table 4. Mean number of prey per stomach and mean stomach fullness index (SFI), with 95% confidence intervals (CI), of juvenile chinook salmon captured in the upper Sacramento River, April–June 1996, arranged by month and size class. Data on number of prey were square-root transformed for calculation of means and confidence intervals, then reverse transformed for presentation.

	Size	Sample	Prey per stomach		SFI (%)	
Month	class (mm)	size	Mean	95% CI	Mean	95% CI
April	30–50	24	23	21–25	3.5	2.6–4.4
	51–70	36	29	27–31	2.0	1.7–2.4
	71–91	23	24	22–27	2.4	1.6–3.2
May	30–50	3	26	20–31	1.8	1.2–2.3
	51–70	31	28	25–30	2.5	1.9–3.1
	71–91	16	26	25–28	1.7	1.4–2.1
June	30–50	2	6	6–7	1.6	1.3–1.9
	51–70	3	24	17–32	1.6	1.4–1.9
	71–91	15	72	66–78	2.1	1.7–2.4

DISCUSSION

Drift Density

Drift density provides a rough index of the secondary productivity of a river. Mean drift density estimates in the Sacramento River (211–2,100 organisms/100 m^3) were comparable to estimates in other rivers and were higher than estimates for systems in which food is considered limiting for drift-feeding salmonids. Bowles and Short (1988) found peak drift densities in a Texas stream to be near 1,000 organisms/100 m^3 in February, 500 in May, 600 in August, and <100 in November. Drift density in the Rakaia River, New Zealand, during freshwater rearing of juvenile chinook salmon was 200–900 organisms/100 m^3 (Sagar and Glova 1988), and, based on the size and condition of fish, food was not limiting. In contrast, drift densities for several southern Appalachian streams were as low as 0.29–27.77 organisms/100 m^3, resulting in food limitation of resident salmonids (Cada et al. 1987).

Relative Abundances of Drift and Diet Taxa

We found the taxonomic composition of the drift and diet of salmon in the Sacramento River was similar to that described for other river systems (Becker 1973, Sagar and Glova 1987) and in a previous study of the upper Sacramento River (Schaffter et al.[2] 1982). As in other large rivers, drift and diet in the Sacramento River were dominated numerically by a few common taxa with a small contribution from other groups. In the Rakaia River, New Zealand, *Deleatidium* (Ephemeroptera: Leptophlebiidae) nymphs made up 85% of the diet of juvenile chinook salmon in the spring; *Deleatidium* constituted about 80% of the benthos and 48% (daytime) to 70% (nighttime) of the drift during spring (Sagar and Glova 1987). During summer, chironomids replaced *Deleatidium* as the most common prey item, though the

abundance of chironomids in the drift did not change substantially from that of spring. In the central Columbia River, juvenile chinook salmon fed mostly on chironomid adults (58–64% of the diet) and larvae (17–18%) (Becker 1973). Notonectidae (Hemiptera) and adult Hydropsychidae were also locally important in the central Columbia River, together making up around 5% of the diet of juvenile chinook salmon. During February–June 1981, the diet of juvenile chinook salmon in the upper Sacramento River (Schaffter et al.[2] 1982) was dominated by chironomids, baetids, and aphids, similar to what was found in our study. In the lower American River, the diet of juvenile salmon consisted primarily of chironomid pupae (50%) and baetid adults (20%) during February–July 1992, and chironomid pupae (54%) and larvae (40%) during February–July 1993 (Merz and Vanicek 1996).

Terrestrial organisms were relatively rare in the Sacramento River drift in spring 1996, constituting about 4% of the total. Estimates of the contribution of terrestrial organisms (primarily Aphididae) to the Sacramento River drift during spring 1981 varied from 0.5% to as much as 50% (Schaffter et al.[2] 1982). Aphids composed from 0.13–38% of the chinook salmon diet during that time. The wide contrast in importance of terrestrial organisms between the 2 studies, and in the Schaffter et al.[2] (1982) study, may reflect sampling during high winds or other riparian disturbances that caused aphids to become trapped in large numbers on the water's surface.

Selection of Available Prey by Juvenile Chinook Salmon

Previous studies have shown prey selection by salmon to be based on size, abundance, and visibility of prey (Higgs et al. 1995). Linear selection indices showed that relatively small organisms, such as cladocerans, collembolans, and chironomid larvae were avoided by juvenile chinook salmon in the Sacramento River. Positively selected items included chironomid pupae and adults, which are seasonally very abundant, and baetid nymphs, which are relatively large as well as abundant. Such factors as surface movements during adult emergence or conspicuous eyespots, in addition to size, may contribute to the greater visibility and, hence, positive selection of these items. Most taxa appeared to be randomly consumed ($L = 0$), or were too rare to allow calculation of L. Concurrent collection of drift and diet information, along with larger sample sizes, would be necessary to provide more reliable estimates of selectivity for rare organisms.

Note that food selection indices are not equivalent to an assessment of absolute preferences for certain taxa, but instead reflect a combination of factors including preference, prior experience, prey detectability, and prey availability. A limitation of all selection indices is that they cannot elucidate the underlying mechanism(s) of the observed patterns of selection (Strauss 1979).

Fish Size, Gape Size, and Prey Size Relationships

As expected, the gape size of juvenile chinook salmon in the Sacramento River increased predictably with fish length. Larger gapes allow salmon to potentially exploit a greater range of prey sizes as they grow. Inclusion of increasingly larger

prey in the diet would be advantageous for growth, assuming that larger prey do not cost more energetically to capture and handle. Field-Dodgson (1988) reported that the mean mouth width of emergent chinook salmon fry (2.2-mm mean gape, range 2.0–2.5 mm; mean fish size 33.5 mm FL) corresponded to the maximum HCW of *Deleatidium* nymphs found in the gut, which suggests that juvenile chinook salmon will consume the largest prey possible. In the Sacramento River, larger salmon ate larger prey on average, but the maximum invertebrate prey sizes in the diet fell considerably short of fish gape potential, as was observed for juvenile Atlantic salmon from Catamaran Brook, New Brunswick (Keeley and Grant 1997). Wainwright and Richard (1995) proposed that pharyngeal gape rather than oral gape may set the limit on the size of prey consumed, which would translate into maximum prey being about half the size of mouth gape. However, as the authors noted, distortion of prey during swallowing complicates that hypothesis. Even if pharyngeal gape determined the size of prey successfully consumed by juvenile chinook salmon in the Sacramento River, maximum HCW of prey still fell considerably short of this limit.

The weak increase of mean and minimum invertebrate prey size with increasing fish size indicates that all juvenile salmon in the upper Sacramento River included small prey items in their diet to meet energy requirements, despite the ability of larger fish to consume larger prey. Essentially, invertebrate prey size was determined more by availability in the environment than by morphological constraints. Though the ability of juvenile salmon to capture fish larvae also appeared to increase as the salmon grew in size, the actual availability of such prey would be only indirectly measurable by drift methods. The relationship between salmon size and piscivory is more complicated, as fish prey are evasive and must be located and pursued, whereas drift feeding is more a process of maintaining a stationary position suitable for intercepting drifting prey. Therefore, with regard to piscivory, gape constraints as well as efficiency in pursuit or handling of fish prey could explain the relationship between predator size and the number of prey consumed.

Feeding Intensity and Stomach Fullness

Total number of items in the stomachs of Sacramento River juvenile chinook salmon was variable depending on fish size and month of capture (Table 4). Due to prey size differences, the SFI provides greater insight into fish energy intake than does total number of items consumed (Hyslop 1980). The mean SFI of juvenile salmon from the Sacramento River was 2.4% of wet weight, comparable to other reports for juvenile chinook salmon feeding in the wild (Sagar and Glova 1988, Brodeur 1992). Brodeur (1992) estimated a geometric mean stomach fullness of 1.34% ($n = 734$) for juvenile chinook salmon off the coast of Washington and Oregon; his range of estimates (0–8%) was very similar to the range in our study (0.5– 8.4%). Sagar and Glova (1988) found mean percent dry weight of food per fish varied between 1.3% and 3.4% for juvenile chinook salmon over one 24-hour period in the Rakaia River, New Zealand. Our estimate does not, however, reflect maximum feeding intensity, as most samples were taken in the morning and early afternoon. Results from a 24-hour study of drift and diet in the Sacramento River indicated maximum

feeding occurred near dusk (Petrusso[9] 1998). Twenty-four-hour consumption by juvenile chinook salmon in that study was estimated as approximately 12.5% of wet body weight, comparable to the 8.3% of dry weight estimated by Sagar and Glova (1988), and corresponding to roughly half the maximum consumption for juvenile salmonids (about 17–20%) (Beauchamp et al. 1989). The estimate reflects reasonably good feeding under natural conditions and is corroborated by condition of juvenile chinook salmon (Petrusso[9] 1998).

CONCLUSIONS

The numeric abundance and taxonomic composition of the food resources in the Sacramento River were comparable to other river systems (Becker 1973; Sagar and Glova 1987, 1988; Bowles and Short 1988). Juvenile chinook salmon appeared to have access to abundant foods, although the largest, most preferred sizes of invertebrates were not always available. As most fall-run fry leave the upper river and arrive at the Sacramento-San Joaquin Delta by April during wet years, food availability during the study period may have increased due to seasonal changes in environmental conditions (increased temperature and water clarity) as well as a reduction in juvenile salmon density (intraspecific competition). Thus, the juvenile salmon that remained during April–June 1996 may have benefited from both factors, and the observed stomach fullness of salmon in the upper river may reflect these favorable conditions. An interesting direction for future studies could be to determine the food availability and energy intake of fall-run juveniles in the upper river during dry years, when emigration is delayed.

ACKNOWLEDGMENTS

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Appendix A. Relative abundance of items in the Sacramento River drift (n = 107 drift samples) and diet of juvenile chinook salmon (n = 153 fish) for the period April–June 1996.

Taxon	Life stage	Drift Number	Drift Percent	Diet Number	Diet Percent
INSECTA					
Collembola	All stages	112	1.08	2	0.04
Ephemeroptera					
Baetidae	Adult	132	1.27	57	1.02
Caenidae	Adult	20	0.19	–	–
Unidentified	Adult	7	0.07	31	0.56
Baetidae	Nymph	1,103	10.61	750	13.44
Heptageniidae	Nymph	10	0.10	6	0.11
Tricorythidae	Nymph	10	0.10	9	0.16
Unidentified	Nymph	8	0.08	11	0.20
Other[a]	All stages	18	0.17	4	0.07
Total Ephemeroptera	All stages	1,308	12.58	868	15.56
Odonata	Nymph	1	0.01	–	–
Orthoptera	Nymph	1	0.01	–	–
Dermaptera	Adult	1	0.01	–	–
Plecoptera					
Perlodidae	Nymph	4	0.04	9	0.16
Unidentified	Nymph	3	0.03	7	0.13
Other[a]	All stages	11	0.11	7	0.13
Total Plecoptera	All stages	18	0.17	23	0.41
Psocoptera	Adult	24	0.23	–	–
Hemiptera					
Corixidae	Nymph	26	0.25	5	0.09
Other[a]	All stages	24	0.23	10	0.18
Total Hemiptera	All stages	50	0.48	15	0.27
Homoptera					
Aphididae	Adult	71	0.68	135	2.42
Cicadellidae	Adult	25	0.24	21	0.38
Coccoidea	Adult	18	0.17	–	–

Appendix 1. (Cont'd)

Taxon	Life Stage	Drift Number	Drift Percent	Diet Number	Diet Percent
Unidentified	Adult	1	0.01	19	0.34
Unidentified	Nymph	13	0.13	6	0.11
Other[a]	All stages	10	0.10	3	0.05
Total Homoptera	All stages	138	1.33	184	3.30
Thysanoptera	All stages	8	0.08	1	0.02
Coleoptera					
Staphylinidae	Adult	24	0.23	9	0.16
Unidentified	Adult	12	0.12	4	0.07
Dytiscidae	Larva	13	0.13	5	0.09
Other[a]	All stages	25	0.24	6	0.11
Total Coleoptera	All stages	74	0.71	24	0.43
Diptera					
Cecidomyiidae	Adult	23	0.22	–	–
Chironomidae	Adult	1,189	11.43	1,587	28.44
Empididae	Adult	2	0.02	39	0.70
Ephydridae	Adult	10	0.10	23	0.41
Simuliidae	Adult	24	0.23	32	0.57
Unidentified	Adult	27	0.26	18	0.32
Chironomidae	Pupa	228	2.19	786	14.09
Simuliidae	Pupa	–	–	12	0.22
Chironomidae	Larva	4,199	40.38	1,175	21.06
Muscidae	Larva	–	–	6	0.11
Simuliidae	Larva	433	4.16	121	2.17
Other[a]	All stages	25	0.24	22	0.39
Total Diptera	All stages	6,160	59.24	3,821	68.48
Trichoptera					
Hydropsychidae	Adult	5	0.05	23	0.41
Hydroptilidae	Adult	7	0.07	8	0.14
Psychomyiidae	Adult	18	0.17	3	0.05
Unidentified	Adult	1	0.01	25	0.45
Brachycentridae	Larva	11	0.11	–	–
Hydropsychidae	Larva	47	0.45	124	2.22
Glossosomatidae	Larva	17	0.16	24	0.43
Psychomyiidae	Larva	11	0.11	1	0.02
Unidentified	Larva	21	0.20	3	0.05
Other[a]	All stages	10	0.10	8	0.14
Total Trichoptera	All stages	148	1.42	219	3.92
Lepidoptera	All stages	4	0.04	–	–
Hymenoptera					
Formicidae	Adult	19	0.18	15	0.27
Unidentified	Adult	73	0.70	73	1.31
Other[a]	All stages	14	0.13	2	0.04
Total Hymenoptera	All stages	106	1.02	90	1.61
TOTAL INSECTA		8,153	78.40	5,247	94.03

Appendix 1. (Cont'd)

Taxon	Life Stage	Drift Number	Drift Percent	Diet Number	Diet Percent
MISCELLANEOUS					
Hydroida		90	0.87	1	0.02
Nematoda		55	0.53	64	1.15
Oligochaeta		595	5.72	9	0.16
Hydracarina		82	0.79	4	0.07
Arachnida		33	0.32	22	0.39
Cladocera					
Bosminidae		11	0.11	–	–
Daphniidae		5	0.05	–	–
Macrothricidae		340	3.27	–	–
Unidentified		142	1.37	6	0.11
Total Cladocera		498	4.79	6	0.11
Eucopepoda					
Calanoida		118	1.13	–	–
Cyclopoida		399	3.84	–	–
Harpacticoida		1	0.01	–	–
Total Eucopepoda		518	4.98	–	–
Teleostei	Larva	352	3.38	147	2.63
Catostomidae	Larva	4	0.04	37	0.66
Total Teleostei		356	3.42	184	3.30
Other[a]		13	0.13	7	0.13
TOTAL MISCELLANEOUS		2,240	21.54	297	5.32
UNIDENTIFIED	All stages	6	0.06	36	0.65
Terrestrial Subtotal		409	3.93	353	6.33
Aquatic Subtotal		9,990	96.07	5,227	93.67
GRAND TOTAL		10,399	100.00	5,580	100.00

[a] Combines taxa making up <0.1% of the drift or diet.

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CONDITION OF JUVENILE CHINOOK SALMON IN THE UPPER SACRAMENTO RIVER, CALIFORNIA

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The physical condition of juvenile chinook salmon, *Oncorhynchus tshawytscha*, rearing in the upper Sacramento River during 1995 and 1996 was compared to the condition of experimentally reared fish. The overall length-wet weight relation for field-caught juvenile salmon was allometric, resulting in a positive relation between condition factor (*K*) and fish size. Mean length, weight, and *K* increased, and mean percent body water decreased, over the study period. Though mean length and weight increased from upstream to downstream sites, there were no distinct spatial trends in *K* or percent body water. Analysis of covariance showed weight at a given length in Sacramento River chinook salmon increased progressively from February through June 1996 for salmon 50–90 mm fork length. Field-caught chinook salmon were generally in better condition, as measured by weight and percent body water at all lengths, than salmon from starved experimental treatment groups.

INTRODUCTION

Fall-run, late-fall-run, winter-run, and spring-run chinook salmon, *Oncorhynchus tshawytscha*, stocks use the upper Sacramento River and its tributaries for spawning. All 4 stocks have declined in an era of numerous anthropogenic changes to the river, such as construction of dams, flow regulation and diversion, stream channelization, conversion of floodplain to agriculture, and gravel extraction (Brown 1991, Fisher 1994). Winter-run chinook salmon are listed as endangered under the federal Endangered Species Act (NMFS[2] 1994), naturally spawned spring-run chinook salmon are classified as threatened (NMFS[3] 1999), and the fall and late-fall stocks are the focus of current protection efforts. Despite extensive research taking place on the Sacramento River to increase understanding of salmon life history and production, condition of juvenile chinook salmon rearing in the upper river has received little attention (Kjelson[4] 1993).

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[1] Present address: 3059-E National Fish Hatchery Road, Hagerman, Idaho 83332.

[2] NMFS. (National Marine Fisheries Service) 1994. Endangered and threatened species; status of Sacramento River winter-run chinook salmon. Federal Register 59:440-450.

[3] NMFS. (National Marine Fisheries Service) 1999. Endangered and threatened species; threatened status for two chinook salmon evolutionarily significant units (ESUs) in California; final rule. Federal Register 64:50393-50415.

[4] Kjelson, M.A. 1993. Emigration. Pages 10-12 *in:* Notes and selected abstracts from the workshop on Central Valley chinook salmon, University of California at Davis, 4–5 January 1993. Department of Wildlife and Fishery Biology, University of California, Davis, California, USA.

Information on the condition of fish serves 2 important purposes. Condition indices such as percent body water or the condition factor (K) provide an assessment of how well fish are coping with their environment (Goede and Barton 1990). Condition indices, therefore, reflect how suitable the environment is for rearing. When viewed as a general measure of energy status or as an indicator of stress (Love 1970, Adams 1990), condition indices may additionally provide insight into the competency of the fish to meet future survival challenges such as food shortages and other similar stressors. For example, percent body water increases during fasting as fat and protein are depleted and, thus, provides an indirect measure of energy storage (Love 1970). Juvenile chinook salmon in the Sacramento River face a number of challenges as they emigrate from upper river habitats, including dams, water diversions, extreme temperature changes, and possible alteration of emigration path associated with anthropogenic changes in hydrology in the Sacramento-San Joaquin Delta. To the extent that measures of fish condition provide a view of both the rearing history and the possible future response of a fish to various stressors, baseline data on the condition of juvenile chinook salmon can be useful to fishery managers in the Sacramento River system.

The main objectives of this study were to 1) determine the physical condition of juvenile chinook salmon in upper river habitats, using condition factor, length-weight relation, and percent body water as indices of condition; 2) compare condition estimates of fish captured in the field with estimates obtained for experimentally reared salmon of known 2-week feeding history; and 3) determine spatial and temporal patterns in condition of field-caught juvenile salmon.

METHODS

Study Sites and Duration

The Sacramento River originates near Mt. Shasta in northern California, and travels approximately 595 river km (rkm) along the floor of the Central Valley to its mouth in the Sacramento-San Joaquin Delta. The northern Central Valley is bordered by the Sierra Nevada and Cascade ranges to the east and the Klamath and Coast ranges to the west. Most precipitation occurs in winter and spring and little or none in summer and fall.

Investigations of the condition of juvenile chinook salmon were conducted at 13 sites on the upper mainstem Sacramento River between the cities of Redding (rkm 481) and Chico (rkm 311) (Fig. 1) during July–August 1995 (brood year 1994) and February–June 1996 (brood year 1995). Samples collected at or downstream of rkm 438 may have included unmarked Coleman National Fish Hatchery (Anderson, California) juvenile chinook salmon. Because of the relatively low abundance of late-fall, winter, and spring-run salmon, fall-run young-of-the-year were used for percent body water estimates, which required sacrificing the fish. Juvenile fall-run chinook salmon were sacrificed for estimates of water content during April–June 1996 only.

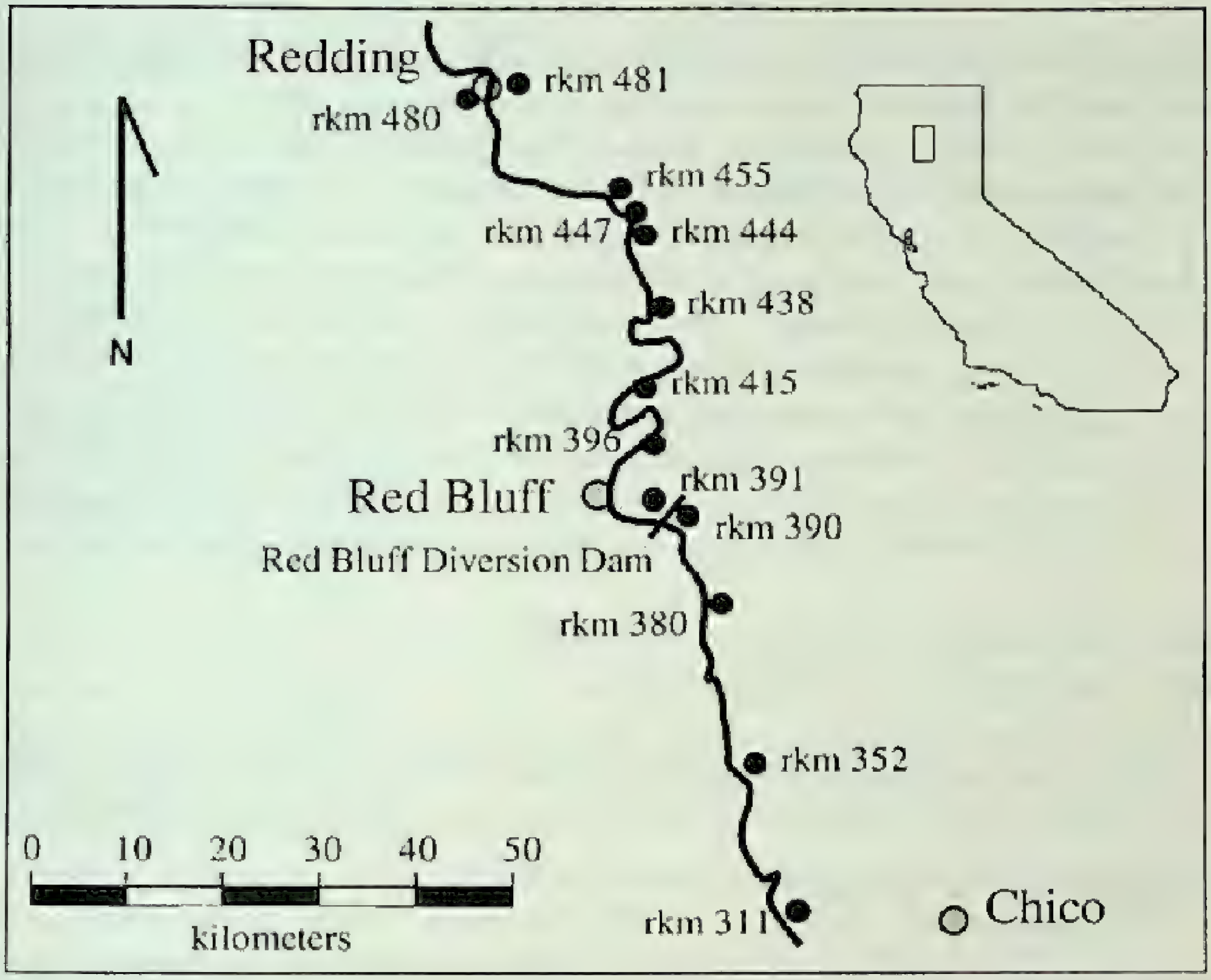

Figure 1. Map of sampling sites for juvenile chinook salmon in the upper Sacramento River, California, 1995–1996.

Fish Collection Methods

Beach Seining

Beach seines (1.21 m x 9.09–22.73 m, 3.2-mm mesh) were used to collect juvenile chinook salmon between 0800 and 1600 hours at each site every other week. Juvenile salmon were anesthetized with tricaine methanesulfonate (MS-222) mixed with river water. Fork length (FL, mm) and wet weight (nearest 0.1 g in 1995 or 0.01 g in 1996) were then measured for each fish. The salmon were blotted with a soft cloth prior to weighing on a portable electronic balance. Run (fall, late-fall, winter, or spring) was assigned based on fish length and date of capture (Fisher[5] 1992, as modified by Greene[6] 1992). On a given sampling date during April–June 1996, up to 20 fall-run salmon per site were euthanized by prolonged exposure to the anesthetic

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[5] Fisher, F.W. 1992. Chinook salmon *Oncorhynchus tshawytscha* growth and occurrence in the Sacramento-San Joaquin river system. California Department of Fish and Game, Inland Fisheries Division, Red Bluff, California, USA.

[6] Greene, S. 1992. Estimated winter-run chinook salmon salvage at the State Water Project and Central Valley Project Delta pumping facilities. Memorandum to R. Brown, 5/8/92. California Department of Water Resources, Sacramento, California, USA.

for use in percent body water analyses. Sacrificed fish were placed in bags of water kept in an ice-filled cooler and later frozen in water.

Due to time constraints in the field, some of the sacrificed fish were measured for length and weight just before transfer to frozen storage rather than at the time of capture, resulting in a measurement delay of 4–11 hours postmortem. Two experimental trials were conducted to develop correction equations that could be applied to delayed measurements. The experiments involved measuring the live weight of fish, storing the fish in bags of water in an ice-filled cooler to mimic conditions in the field, and measuring postmortem weights periodically for up to 12 h. Regression equations developed from the combined results of the experiments ($n = 80$ fish) were used to convert delayed measurements from fish in the field to live length and weight estimates. The following correction equations were used:

Length: $y = 1.0237x - 0.7154$, $r^2 = 0.98$, and
Weight: $y = 0.9672x + 0.0188$, $r^2 = 0.99$,

where x is the postmortem (delayed) length or weight and y is the estimated live length or weight. Corrections were applied to the measurements of 445 out of 1,204 fish.

Other Methods of Fish Capture

Lengths and weights of juvenile salmon, and samples of fall-run juveniles, were also collected once per month during April–June 1996 at 2 rotary screw traps (rkm 447) operated by the California Department of Fish and Game.

Experimental Growth

Experiments with Hatchery Salmon

Two separate growth trials were conducted to compare fish of known feeding history with fish captured in the field. Each experimental trial included 1 fasted treatment group and 1 or 2 fed treatment groups (Table 1). Experiment I had 2 treatments in which the fish were fed, whereas Experiment II had only 1 fed treatment group. The experiments were conducted at different times of the year, and therefore, differed in the size range of fish used.

Coleman National Fish Hatchery brood year 1995 fall-run chinook salmon were held at the U.S. Bureau of Reclamation Fish Holding Facility, Red Bluff, California, in 780-liter fiberglass circular tanks supplied with aerated 16°C well water. Each treatment in growth experiments I and II began with approximately 300 fish per tank. BioMoist Grower pellets (Bio-Oregon, Inc.[7], Warrenton, Oregon, USA) were distributed to treatment groups on a 12-h belt feeder (1.0–2.4-mm pellets were used, depending on fish size). Initial rations were calculated based on the length-weight

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[7] Use of trade names does not imply endorsement by the California Department of Fish and Game.

Table 1. Summary of treatment information for growth experiments with brood year 1995 juvenile fall-run chinook salmon from the Coleman National Fish Hatchery. Starting date of Experiment I was 1/19/96, that of Experiment II was 4/30/96.

Treatment information	Experiment I	Experiment II
Number of treatments	3	2
Ration level (percent body weight fed per day)		
Treatment 0 (Zero ration)	0%	0%
Treatment 1 (Low ration)	2–5%	3–4%
Treatment 2 (High ration)	4–10%	Not applicable
Initial number of fish per tank	300	300
Mean initial FL of experimental fish (mm)	44	68
Initial FL range (mm)	40–47	58–75
Duration of treatment (days)	16	15

relations of initial subsamples of fish, and the rations were adjusted according to the number of fish remaining in each tank after subsamples were removed. The zero-ration treatments were halted after approximately 2 weeks, before fasting-induced mortality could occur.

A random subsample of 10–20 fish was selected from each tank at the beginning of the experiment and weekly thereafter. Fish were anesthetized with MS-222 until dead and were measured for fork length (mm) and wet weight (nearest 0.01 g) with the same equipment and methods used in the field. The carcasses were placed in bags of water and then frozen.

Condition Estimates

Condition Factor

The lengths and weights of field-caught and experimental juvenile chinook salmon were used to calculate the condition factor (K) for each fish, with the equation:

$K = 10^5 \times$ (wet weight / fork length^3).

Percent Body Water

Frozen salmon were thawed in the laboratory, and fork lengths (mm) and wet weights (mg) were recorded. Fish were dried to a constant weight in a drying oven at 70°C and the dry weight (mg) of each fish was recorded. Because fish were not tracked individually prior to thaw, their live length and weight measurements were estimated from thawed lengths and weights using regressions calculated from fish in the postmortem experiments (n = 80). The equations used to convert thawed to live measurements are as follows:

Length: $y = 1.0357x + 0.9421$, $r^2 = 0.99$, and
Weight: $y = 0.9337x + 0.0218$, $r^2 = 0.99$,

where x represents thawed measurements, and y represents estimated live measurements. Percent body water was estimated with the equation:

Percent body water = 100 x {[ELW – DW] / ELW},

where ELW = the estimated live wet weight (g) of fish and DW = dry weight (g).

Statistical Methods

Least squares regression was used to describe length-wet weight and length-percent body water relations. The length-weight data were $\log_e$ (ln) transformed to linearize relations and stabilize error variance. Length, weight, condition factor (*K*) and percent body water of fish captured in the field were analyzed in relation to month and river kilometer of capture using the SAS general linear model function (GLM), which performs a generalized analysis of variance appropriate for unbalanced data (SAS Institute 1989). Length-wet weight and length-percent body water relations of samples pooled by month and site of capture were compared using the slope heterogeneity test and analysis of covariance (ANCOVA) in SAS (Littell et al. 1991). Fish <50 mm FL and >90 mm FL were excluded from length-wet weight slope heterogeneity tests as they affected the linearity of the regressions. A significance level of 0.05 was used in statistical tests.

RESULTS

Length-Weight and Length-Condition Factor Relations

The overall regression of ln wet weight on ln length for juvenile salmon captured from the Sacramento River was described by the equation y = 3.4852x – 6.6088 (F = 129,326; df = 1, 1202; P = <0.001) (Fig. 2). The allometric length-weight relation, characterized by a regression slope b greater than 3.0, resulted in a curvilinear relation between length and condition factor (*K*) (Fig. 3), with values of *K* increasing with increased length until a decline at sizes >80 mm.

Field-caught salmon were generally heavier at any given length than fish experimentally fasted for 2 weeks, but slightly lighter at a given length than fish in fed treatment groups (Fig. 4). The crossing of the Experiment II low ration regression over the field regression (Fig. 4) indicated some overlap in weight-at-length. Among experimental groups, weight at a given length increased with ration level. Slopes of the ln length-ln weight regressions for fasted groups were high (3.5225 for Experiment I and 4.0178 for Experiment II), whereas slopes for fed groups were below 3.0.

Length-Percent Body Water Relation

The length-percent body water relation of juvenile chinook salmon collected in the field showed a decrease in percent body water with increasing length (y = 0.144x + 90.516) (F = 533; df = 1, 515; P <0.001)) (Fig. 5). Length-percent body water relations for experimental fish showed that zero-ration treatments had

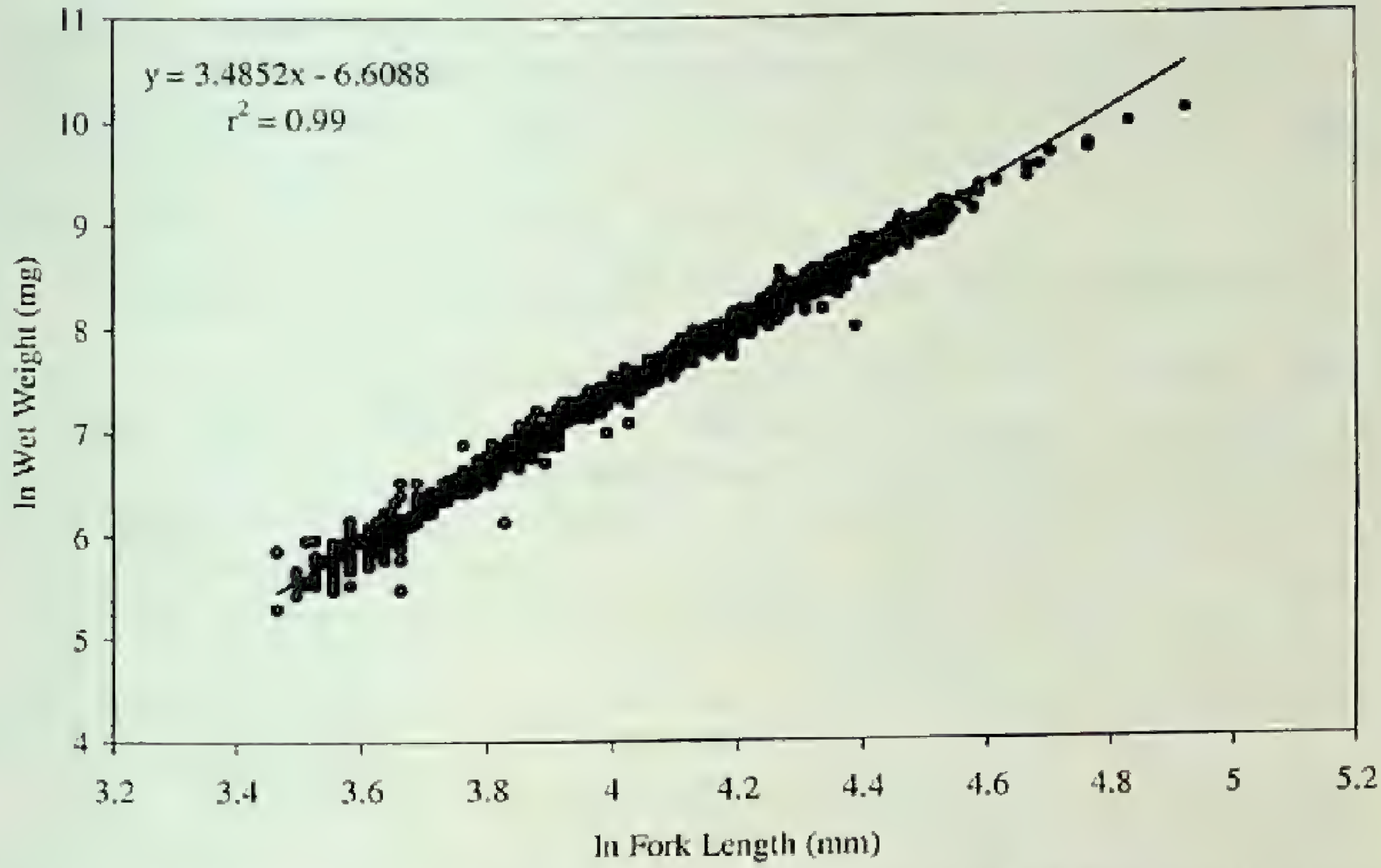

Figure 2. Regression of ln wet weight on ln fork length of juvenile chinook salmon captured from the upper Sacramento River, 1995–1996 (n = 1,204).

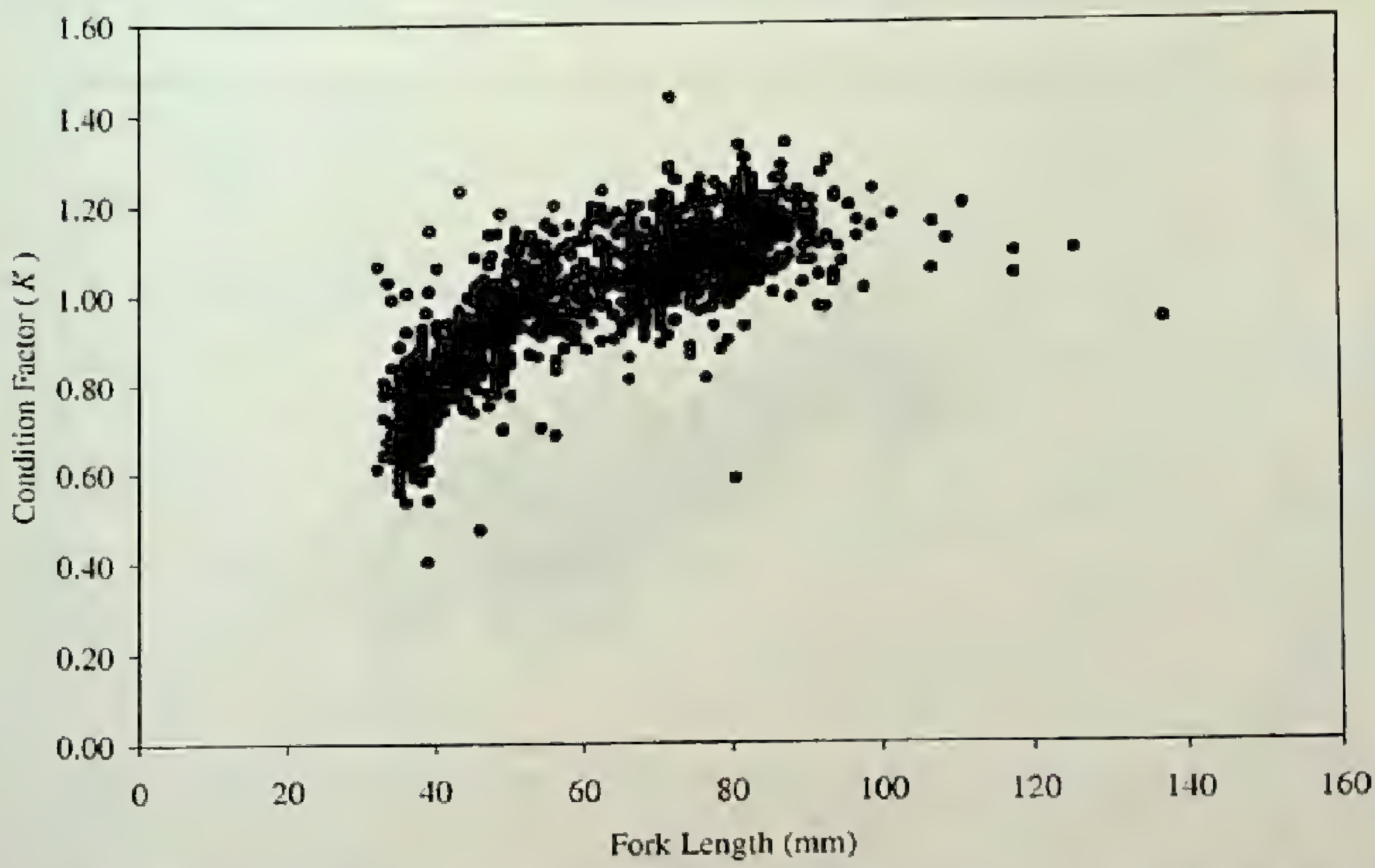

Figure 3. Relation between condition factor (K) and fork length of juvenile chinook salmon captured from the upper Sacramento River, 1995–1996 (n = 1,204).

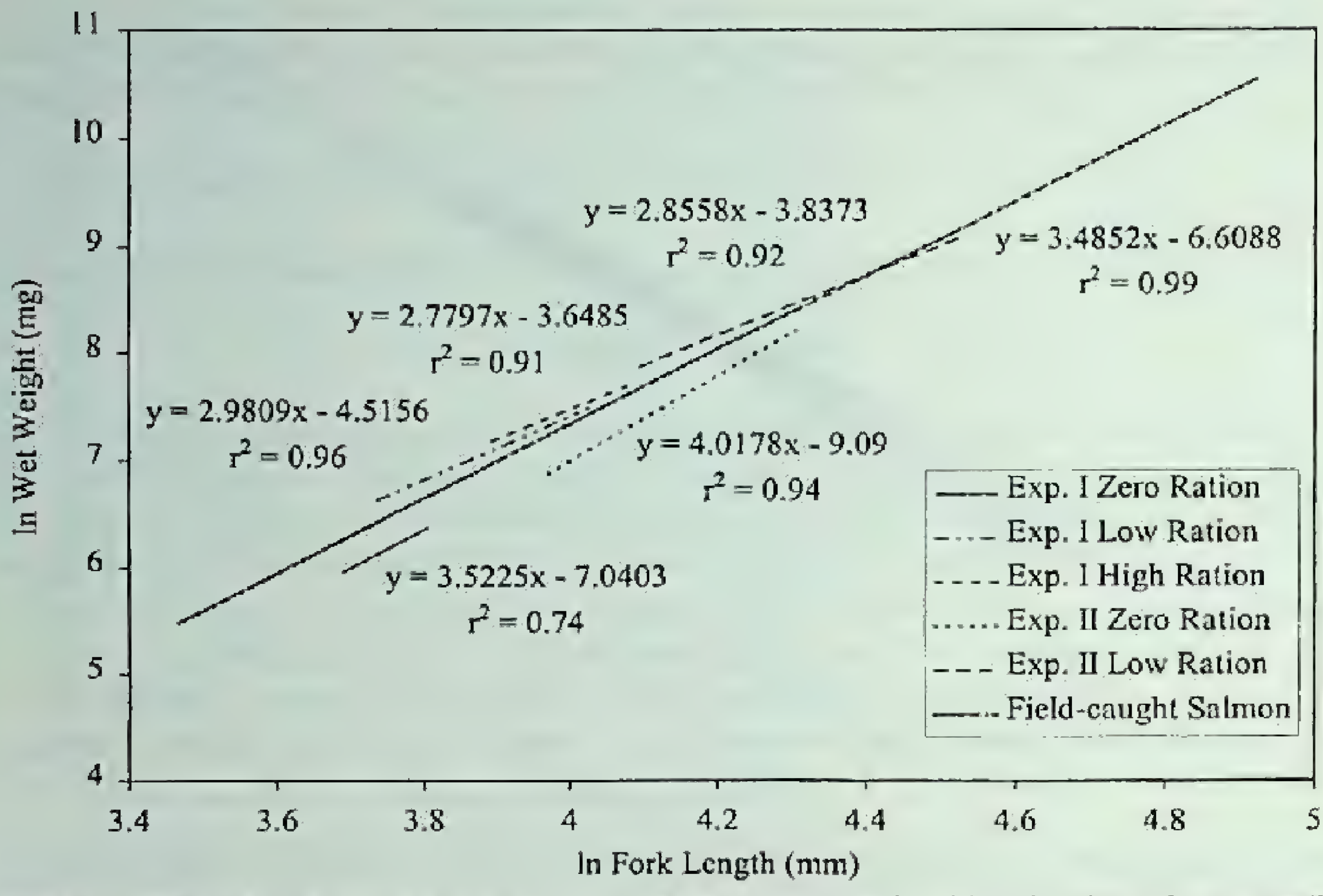

Figure 4. Regressions of ln wet weight on ln fork length of juvenile chinook salmon from growth experiments, compared with the regression for juvenile chinook salmon captured from the Sacramento River, 1995–1996 (field-caught salmon).

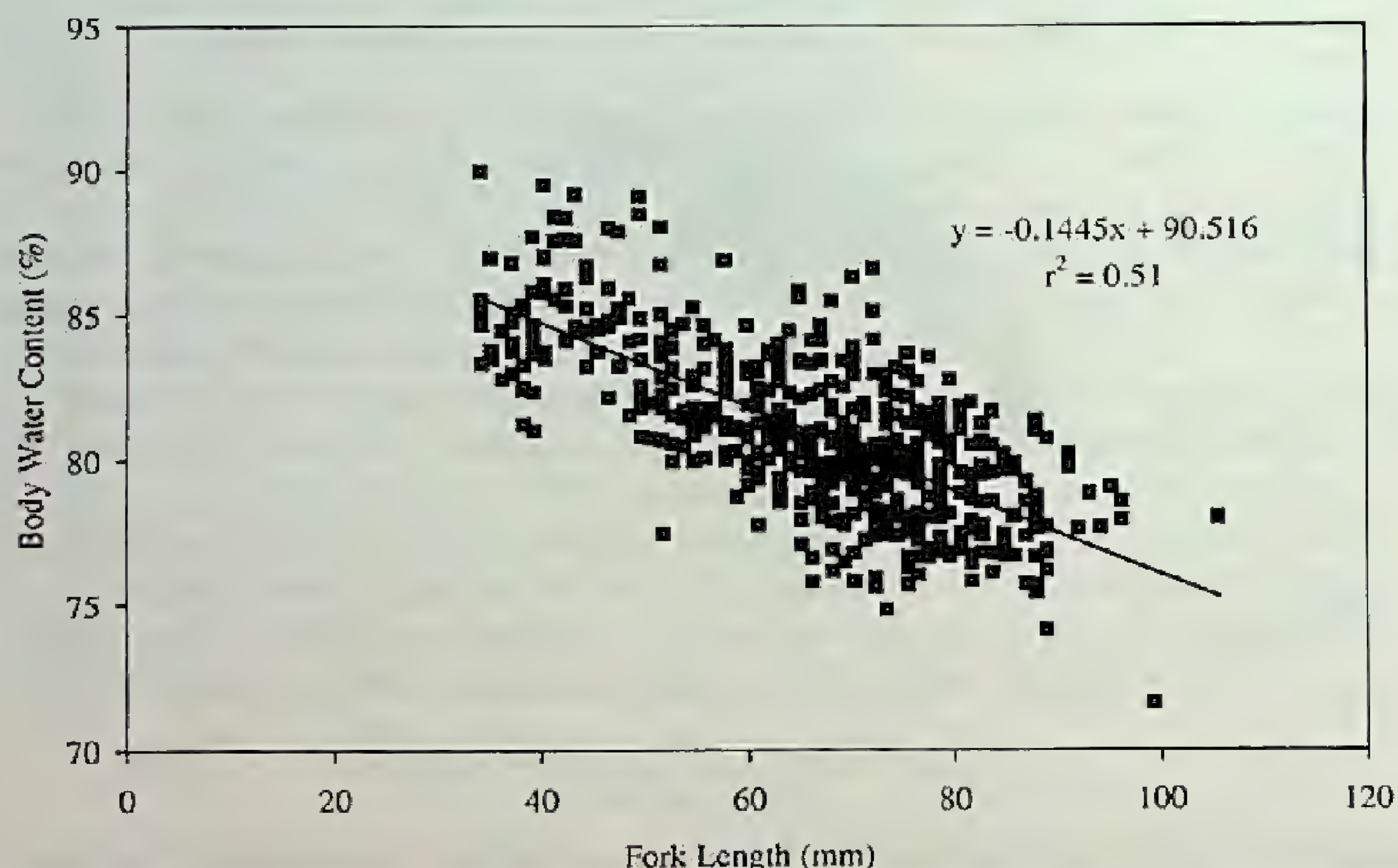

Figure 5. Regression of percent body water on fork length of juvenile chinook salmon captured from the Sacramento River, April–June 1996 (n = 517).

the highest percent body water for a given length and the fed treatments had the lowest (Fig. 6). As with the length-weight relation, percent water at a given length for field-caught salmon was intermediate between that of fasted and fed groups; however, the Experiment I low ration group overlapped the field regression at its initial lengths (Fig. 6).

General Linear Model Analysis of Spatial and Temporal Patterns

General linear model analysis indicated that the month and river kilometer effects on length, weight, condition factor K and percent body water were significant (P <0.0001 across all variables for both terms) with coefficients of determination (r^2) of 0.36, 0.30, 0.39, and 0.24 (Table 2). The month x river kilometer interaction effects, though significant, were excluded from the analyses, as the absence of some month-river kilometer combinations prevented meaningful interpretation. When included, interaction terms in the models accounted for little extra variation in the dependent variables (r^2 were 0.41, 0.34, 0.43, and 0.34 for length, weight, condition factor, and percent body water).

Least squares (adjusted) mean length and weight determined by the GLM analyses (Littell et al. 1991) generally increased from upstream to downstream sites, and from winter to summer months (Tables 3 and 4). Least squares mean condition factor increased over time, from 0.82 in February 1996 to 1.15 in June 1996 (Table 3). Spatial trends in mean condition factor were not as apparent, with only slight differences among sites; however, mean condition factors below 1.0 were associated

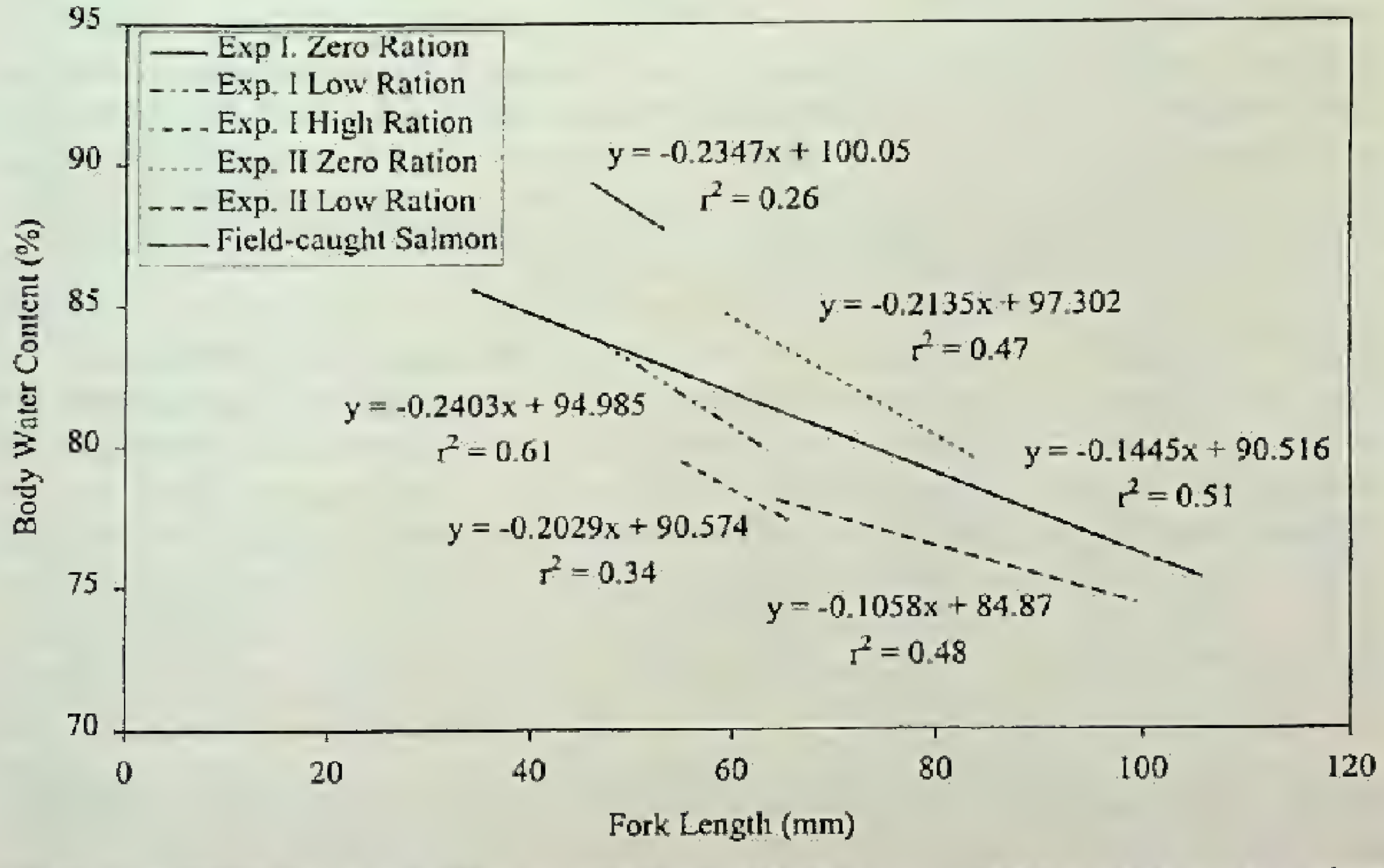

Figure 6. Regressions of percent body water on fork length of juvenile chinook salmon from growth experiments, compared with the regression for juvenile chinook salmon captured from the Sacramento River, April–June 1996 (field-caught salmon).

Table 2. Results of general linear model analyses, describing the effect of month and river kilometer (rkm) of capture on length, wet weight, condition factor (K) and percent body water of juvenile chinook salmon captured from the Sacramento River, 1995–1996 (n = 1,204 for length, weight, and K; n = 517 for percent water). CV is the coefficient of variation.

Variable	Factor/source	df	F-ratio	P	r^2	CV%
Length	Model	16	41.20	0.0001	0.36	24.80
	Main effects					
	Month	5	83.06	0.0001		
	Rkm	11	6.26	0.0001		
Weight	Model	16	31.17	0.0001	0.30	80.10
	Main effects					
	Month	5	68.91	0.0001		
	Rkm	11	4.45	0.0001		
Condition (K)	Model	16	47.83	0.0001	0.39	13.63
	Main effects					
	Month	5	93.48	0.0001		
	Rkm	11	9.05	0.0001		
Percent body water	Model	9	17.58	0.0001	0.24	3.15
	Main effects					
	Month	2	51.87	0.0001		
	Rkm	7	10.53	0.0001		

Table 3. Least squares mean length, weight, condition factor (K), and percent body water (with standard errors in parentheses) of Sacramento River juvenile chinook salmon by month of capture, averaged across all sites. The estimates were produced by general linear model analyses (n = 1,204 for length, weight, and K; n = 517 for percent body water). Delayed length and weight data were converted to live estimates by regression.

Brood Year	Capture date	Fork length (mm)	Weight(g)	Condition factor (K)	Percent body water
1994	July 1995	75 (2)	5.28 (0.31)	1.06 (0.02)	No data
1995	Feb 1996	44 (1)	1.33 (0.18)	0.82 (0.01)	No data
1995	Mar 1996	47 (2)	0.99 (0.30)	0.92 (0.02)	No data
1995	Apr 1996	58 (1)	2.31 (0.16)	0.96 (0.01)	82.04 (0.18)
1995	May 1996	65 (1)	3.26 (0.21)	1.06 (0.01)	79.96 (0.25)
1995	June 1996	76 (2)	5.61 (0.26)	1.15 (0.02)	78.75 (0.40)

with sites upstream of rkm 391, whereas fish sampled at sites below that point had mean condition factors above 1.0 (Table 4). Least squares mean percent body water decreased over time (Table 3) but exhibited no clear pattern with respect to river kilometer (Table 4).

Table 4. Least squares mean length, weight, condition factor (K), and percent body water (with standard errors in parentheses) of Sacramento River juvenile chinook salmon by site (river kilometer [rkm]), averaged across months of capture. Estimates were produced by general linear model analyses (n = 1,204 for length, weight, and K; n = 517 for percent water). Delayed length and weight data were converted to live estimates by regression. Percent body water was calculated based on data from juveniles captured April–June 1996.

Site (rkm)	Fork length (mm)	Weight (g)	Condition factor (K)	Percent body water
480	54 (3)	2.04 (0.42)	0.95 (0.02)	No data
455	54 (3)	2.22 (0.42)	0.95 (0.02)	No data
447[a]	59 (1)	3.23 (0.17)	0.95 (0.01)	79.20 (0.22)
444	58 (6)	2.99 (0.96)	0.98 (0.06)	No data
438	58 (3)	2.66 (0.43)	1.02 (0.03)	82.46 (0.51)
415	58 (2)	2.93 (0.32)	0.97 (0.02)	80.92 (0.76)
396	62 (2)	3.07 (0.30)	0.98 (0.02)	79.41 (0.43)
391	68 (2)	4.43 (0.30)	1.05 (0.02)	No data
390	65 (2)	3.36 (0.32)	1.02 (0.02)	77.99 (0.68)
380	62 (1)	3.12 (0.16)	1.02 (0.01)	80.44 (0.28)
352	65 (1)	3.64 (0.20)	1.02 (0.01)	81.20 (0.32)
311	66 (1)	3.87 (0.20)	1.05 (0.01)	80.38 (0.29)

[a] Rotary screw trap site; all other data collected by beach seine.

Analysis of Covariance of Spatial and Temporal Patterns

Because condition factor and percent body water GLM results were strongly dependent on mean length of fish sampled, the question remained whether weight or percent body water for a given length differed between months or sites. Slope heterogeneity tests indicated that slopes of the ln length-ln weight regressions by month and river kilometer were not significantly different for the 50–90-mm size range when fish from July 1995 were excluded; therefore, ANCOVA was used to compare intercepts of fish of this size range captured in 1996 (n = 623 for months; n = 621 for sites). Intercepts were significantly different among months (P <0.0001) and sites (P <0.0001). Slopes of the length-percent body water relations were homogeneous between months, but heterogeneous between sites (P = 0.003; n = 517). Tables 5 and 6 summarize the length-weight and length-percent body water regression parameters by month and river kilometer. In cases where slopes were homogeneous and intercepts were significantly different, higher intercepts indicated more weight ("better" condition) or a greater proportion of water ("worse" condition) for a given length. For length-weight relations by month in 1996, the pooled slope (3.1796) was accompanied by intercept values that increased incrementally each month from February (–5.4149) to June (–5.2342) (Table 5). Length-percent body water relations showed a different result: fish captured in May had the best water content (lowest intercept, a = 89.3318), followed by June and then April (pooled slope b = –0.1362) (Table 5). For the analysis by site (rkm), no clear progression in length-weight intercept value from upstream to downstream, given a pooled slope of 3.2389, was

apparent (Table 6). Note that the ranges of y-intercept values in Tables 5 and 6 represent small absolute differences in weight or percent body water.

Table 5. Slopes and intercepts for ln length-ln weight regressions for fish 50–90 mm FL and length-percent body water regressions by month for juvenile chinook salmon captured from the Sacramento River, 1995–1996 (n = 623 for length-weight; n = 517 for length-water). Pooled slopes were estimated by slope heterogeneity tests. Intercepts, determined by analysis of covariance (ANCOVA), are ranked from highest to lowest for weight, and from lowest to highest for percent body water. Data from July 1995 were excluded from the ANCOVA due to difference in slope, but regression parameters are presented for comparison. Ln L = Ln length and Ln W = Ln weight. Numbers in parentheses are ANCOVA ranks.

Brood year	Capture date	Ln L-Ln W slope or pooled slope (b)	Ln L-Ln W intercept (a)	Length-percent body water pooled slope (b)	Length-percent body water intercept (a)
1994	Jul 1995	3.5362	–6.8393	No data	No data
1995	Feb 1996	3.1796	–5.4149 (5)	No data	No data
1995	Mar 1996	3.1796	–5.3497 (4)	No data	No data
1995	Apr 1996	3.1796	–5.3166 (3)	–0.1362	90.3157 (3)
1995	May 1996	3.1796	–5.2924 (2)	–0.1362	89.3318 (1)
1995	Jun 1996	3.1796	–5.2342 (1)	–0.1362	89.5674 (2)

Table 6. Slopes and intercepts for ln length-ln weight regressions for fish 50–90 mm FL and length-percent body water regressions by river kilometer (rkm) for juvenile chinook salmon captured in the Sacramento River in 1996 (n = 621 for length-weight; n = 517 for length-water). The length-weight pooled slope (3.2389) was estimated by a slope heterogeneity test. Length-weight intercepts, determined by analysis of covariance (ANCOVA), are ranked from highest to lowest. Both slopes and intercepts are reported for the length-percent body water regressions due to heterogeneity of slopes. Ln L = Ln length and Ln W = Ln weight. Numbers in parentheses are ANCOVA rank.

Site (rkm)	Ln L-Ln W intercept (a)	Length-percent body water slope (b)	Length-percent body water intercept (a)
447[a]	–5.5565 (6)	–0.1388	89.4373
438	–5.5416 (4)	–0.1177	90.4213
415	–5.6003 (8)	–0.1493	91.3032
396	–5.6063 (9)	–0.1391	89.3011
391	–5.5344 (2)	No data	No data
390	–5.5939 (7)	–0.0983	87.9603
380	–5.5311 (1)	–0.1633	91.4561
352	–5.5489 (5)	–0.0987	88.6904
311	–5.5396 (3)	–0.2020	94.8743

[a] Rotary screw trap site; all other data collected by beach seine.

DISCUSSION

Condition of Field-Caught Juvenile Chinook Salmon

Length-Weight and Length-Condition Factor Relations

The length-weight relation for juvenile chinook salmon captured in the Sacramento River was characterized by a slope greater than 3.0. Length-weight relations have been used to compare condition of fish samples or populations (Cone 1989) and to represent changes in body form over ontogeny (Safran 1992). Some authors assume that the length-weight regression line is unidirectional, with growth in weight proceeding from the smallest length, and with breaks in the regression delineating growth stanzas (LeCren 1951, Wootton 1992). Using the regression slope to designate instantaneous samples as representing "isometric" ($b = 3.0$) or "allometric" ($b \neq 3.0$) growth (e.g., see Cone's response in Springer et al. 1990) may be incorrect. Godinho (1997) recognized that variations in the slope of the length-weight relation for the hatchetfish, *Triportheus guentheri*, could occur if individuals of different lengths experienced weight changes of differing rates or directions. Fasted experimental groups in our study exhibited the highest length-weight slopes (Fig. 4), providing evidence that the slope does not always indicate growth form for a population. Condition of populations should be compared by the entire length-weight relation given the limitations of using only the slope or intercept (Bolger and Connolly 1989, Cone 1989).

Because the slope of the length-weight relation exceeded 3.0, the observed range of condition factors for Sacramento River salmon differed between length classes (Fig. 3). However, as just discussed, a slope >3.0 in the length-weight relation of a sample does not prove that the assumption of isometric growth, considered necessary for proper use of K (LeCren 1951, Cone 1989), has been violated. The greater limitation of the condition factor is that it does not allow visualization of true differences in weight-at-length between samples or populations. Our estimates of condition factor for juvenile chinook salmon in the mainstem Sacramento River were similar to estimates reported for juvenile chinook salmon in other systems (Carl 1984, Hard 1986, Field-Dodgson 1988), in intermittent tributaries of the Sacramento River (Moore[8] 1997), and in the lower American River (Snider and Titus[9, 10] 1995,

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[8] Moore, T.L. 1997. Condition and feeding of juvenile chinook salmon in selected intermittent tributaries of the upper Sacramento River. M.S. Thesis, California State University, Chico, California, USA.

[9] Snider, B. and R.G. Titus. 1995. Lower American River emigration survey, November 1993–July 1994. Stream Flow and Habitat Evaluation Program Report, California Department of Fish and Game, Environmental Services Division, Sacramento, California, USA.

[10] Snider, B. and R.G. Titus. 1996. Fish community survey, lower American River, January through June 1995. Stream Flow and Habitat Evaluation Program Report, California Department of Fish and Game , Environmental Services Division, Sacramento, California, USA.

1996; Snider et al.[11] 1997).

Condition factors are often used to estimate the energy status of fish, and attempts have been made to relate condition factor to percent fat, energy density, and other components of proximate analysis, with varying results (Caulton and Bursell 1977, Weatherley and Gill 1983, Herbinger and Friars 1991, Salam and Davies 1994, Jonas et al. 1996). Condition factors in juvenile fishes may be related to proximate components because all factors vary with fish size. However, an extremely low (size-specific) condition factor does reflect ecologically relevant differences in energy status. In our study, experimental juveniles that were starved for 2 weeks had low condition factors, were lethargic, and appeared to be swimming more slowly than fish in fed treatment groups. The ability of the starved fish to escape predation and to locate and capture prey may have been very limited upon release into the demanding river environment. However, with increased food availability and in the absence of high energy demand, starved juvenile salmonids can recover and compensate with rapid growth and increased condition (Weatherley and Gill 1981, Petrusso[12] 1998).

Length-Percent Body Water Relation

The length-percent body water relation is useful for representing true energy differences among sizes. Percent body water, or percent dry weight, can be used to estimate seasonal changes in energy density of fish with reasonable confidence (Hartman and Brandt 1995, Jonas et al. 1996), due to the fact that changes in dry weight primarily reflect changes in fat, the most important energy store in fishes (Hayes and Taylor 1994). Given the relation between percent body water and energy, the decrease in percent body water over the range of lengths (Fig. 5) indicates that larger juvenile salmon had greater proportions of energy and lower proportions of body water, and hence greater energy densities, than smaller fish. Similar patterns were seen for condition factor, with larger fish displaying higher condition factors than smaller fish.

What is the adaptive significance of length-related differences in body composition? One possible explanation has to do with predation risk or competitive interactions (Gardiner and Geddes 1980). Salmon fry are more vulnerable to predation due to small size and undeveloped swimming ability. However, a relatively high proportion of body weight in water may function to increase overall bulk when food is limited, making the difference between survival and predation by gape-limited piscivores. Bulkier fish may also be more likely to "win" in competitive interactions.

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[11] Snider, B., R.G. Titus, and B.A. Payne. 1997. Lower American River emigration survey, November 1994–September 1995. Stream Flow and Habitat Evaluation Program Report. California Department of Fish and Game, Environmental Services Division, Sacramento, California, USA.

[12] Petrusso, P.A. 1998. Feeding habits and condition of juvenile chinook salmon in the upper Sacramento River, California. M.S. Thesis, Michigan State University, East Lansing, Michigan, USA.

As the salmon grow to smolt sizes, swimming ability develops, and avoidance of predation by avian and other non-gape-limited predators depends more upon a quick escape than upon bulk. Therefore, a streamlined body (without the water bulk) associated with smolting and preparation for ocean existence has its advantages in freshwater rearing. Differences in body composition among sizes may be associated with the different risks of being large versus small.

Comparison of Field-Caught and Experimental Salmon

Because length-weight regression parameters for juvenile chinook salmon are not commonly reported in the literature, juvenile salmon of known rearing history from growth experiments provided a useful standard of comparison. Field-caught salmon were heavier at all lengths than juvenile salmon that were fasted for 2 weeks, but generally lighter than juveniles fed a pelleted diet. The fact that wild juvenile chinook salmon were heavier and therefore in better condition than fasted fish of similar length indicates that environmental conditions were conducive to feeding and growth. Such a result corroborates findings on stomach fullness in Sacramento River chinook salmon (Petrusso[12] 1998), which suggest that juveniles, while not feeding at maximum rates, were maintaining an adequate level of energy intake. Juvenile chinook salmon captured in the field had lower percent body water (more stored energy) for a given length than experimental fish from fasted treatments and higher percent body water than experimental fish from fed treatments (Fig. 6), which accords with results from the length-weight relation. Experimental salmon fed low and high rations were in better condition than juvenile chinook salmon captured from the Sacramento River; however, this may be partly explained by differences both in quality of food and in energy demands between experimental and field-caught fish. At a constant 16°C, water temperature in the experiments was higher than water temperatures measured in the study area during February and March, but similar to temperatures at sites downstream of Red Bluff Diversion Dam from April through July. Upstream sites between Bend Bridge (rkm 415) and Keswick Dam (rkm 486) are maintained below 13.3°C from April 15 to August 31 to benefit winter-run chinook salmon spawning habitat (NMFS[2] 1994).

Spatial and Temporal Trends in Condition

The patterns of salmon length, weight, condition factor and percent body water estimated by the least squares means (GLM analysis) suggest that environmental conditions were conducive to fish growth and increased condition over time and as the fish migrated downstream. However, condition in the GLM analysis was partially confounded with length due to the unequal representation of size classes in samples from different months or sites. Though it provided a reasonable representation of spatial and temporal condition patterns in this study, the GLM may work best in situations uncomplicated by the protracted, overlapping emergence times of several stocks.

Use of ANCOVA to compare salmon weight or percent body water at a given length between months and sites confirmed some patterns from the GLM analysis and suggested differences in others. Weight-at-length (for fish 50–90 mm) increased from February through June 1996 (Table 5), which may reflect a progressive increase in temperature, photoperiod, and food availability during that period. However, trends in percent body water at a given length were not consistent across the 3 months for which data were available, April–June 1996. The highest intercept estimate of percent body water (which would indicate lowest energy density, or poorest condition) was for April, and the lowest was for May. Though ANCOVA indicated statistically significant differences, the ranges in monthly intercepts were small, translating into a 4-mg difference in weight-at-length and 0.98% difference in percent body water-at-length. The biological significance of such differences in condition has yet to be demonstrated in performance measures. Weight for a given length indicated no clear spatial trends in condition, although higher ranks were generally associated with downstream sites (Table 6). The range of length-weight intercepts for sites (0.3 mg) was even narrower than that of monthly intercepts. Whereas the mainstem Sacramento River is generally cooler at upstream sites nearer Keswick Dam water releases, the availability of warmer tributaries and backwaters for rearing along the entire length of the study area may explain the variable estimates in weight-at-length from upstream to downstream.

Results of the GLM and covariance analyses were possibly complicated by the presence of large numbers of newly released hatchery fish in areas of the system below Coleman Hatchery release points. About 7.5 million unmarked fall-run fry and 12.3 million smolts (8% marked) were released during the study period in 1996, either into Battle Creek (confluence at rkm 438) or at rkm 390 below Red Bluff Diversion Dam (S. Croci, U.S. Fish and Wildlife Service, personal communication). Hatchery fish released as fry, that rear in the upper river for an extended period, can still provide useful information on habitat suitability, assuming these fish are able to develop similar behaviors as salmon spawned in the river. Unmarked smolts that pass through the upper river quickly and whose condition is solely representative of the hatchery rearing environment would cause the most difficulty in data interpretation. Discontinuity in spatial condition patterns indicative of hatchery influence was not apparent in our results (Table 4).

CONCLUSIONS

The length-weight relations, condition factors, and estimates of percent body water of juvenile chinook salmon in the upper Sacramento River indicate that environmental conditions should be generally favorable for growth and robustness during wet years similar to 1995 and 1996. Wet years are characterized by an increase in habitat and greater lateral habitat complexity in the form of backwaters and intermittently flowing tributaries, as compared with dry years (Schlosser 1991). Though it was not possible to separate fish in this study based on the primary habitat(s) responsible for growth (hatchery, tributary, mainstem, or a combination of these), field-caught salmon in general were in better condition (heavier at all lengths) than salmon starved for 2 weeks

under experimental conditions. The growth experiments also revealed that the smallest salmon may be the most affected by food limitation. Still, in a separate study of juvenile chinook salmon rearing in tributaries of the Sacramento River in 1996 (Moore[8] 1997), fish reportedly grew at rates near the published maximum for juvenile chinook salmon in the wild. An interesting question, unanswerable with our data, concerns the condition of juvenile salmon during dry and critically dry years. Dry years would presumably be characterized by lower habitat quantity and quality. Future studies could focus on comparing the growth and condition of fish in different water years in different parts of the Sacramento River (upper, middle, lower) and the delta.

Based on our results, juvenile chinook salmon reared in the upper river were relatively competent, in an energetic sense, to withstand some of the natural stressors encountered during emigration. Energy status only partially determines a fish's ability to survive, however, particularly when water development in the river is considered. Mortality risk may be higher for smaller salmon, even those in relatively good condition for their size, due to greater vulnerability to piscivorous fish waiting below dams (Garcia[13] 1989) and lower screening efficiency at water diversions (Clark and Strong 1991). Other factors, such as elevated water temperatures in the lower river, delta water diversions, and entrainment in delta pumps may reduce salmon survival regardless of condition (Kjelson and Brandes 1989).

Our study suggests a more critical approach to the use of condition factors for comparing samples or populations, one that involves analysis of length-weight and length-percent body water relations where possible, as well as the reporting of both regression parameters. If salmon stocks in the Sacramento River continue to decline, the availability of baseline data on condition will become increasingly important, and should be made available in a variety of forms beyond the standard reporting of mean condition factor.

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[13] Garcia, A. 1989. The impacts of squawfish predation on juvenile chinook salmon at Red Bluff Diversion Dam and other locations in the Sacramento River. USFWS Report No. AFF/FAO-89-05. U.S. Fish and Wildlife Service Fisheries Assistance Office, Red Bluff, California, USA.

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GUT CONTENTS OF JUVENILE CHINOOK SALMON FROM THE UPPER SACRAMENTO RIVER, CALIFORNIA, DURING SPRING 1998

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During the planning phase of a field investigation on heavy-metal contamination of chinook salmon, *Oncorhynchus tshawytscha*, and their food supply in the upper Sacramento River (see Saiki[1] 2000 for findings from that investigation), we found only 4 references dealing with food habits of juvenile salmon in the river and its tributaries below Keswick Dam. Rutter (1904) recorded the gut contents of 210 fish from the Sacramento River and its tributaries between Sullaway Creek (located upstream from Dunsmuir) and Rio Vista during 1898–1899. Schaffter et al.[2] (1983) summarized the gut contents of 466 juvenile salmon from the Sacramento River between Red Bluff and Chico during 1981. Merz and Vanicek (1996) described the gut contents of 468 juvenile salmon from the lower American River between Nimbus Dam and its confluence with the Sacramento River during 1992–1993. Finally, Moore[3] (1997) examined the gut contents of 16 juvenile salmon from the Sacramento River at Red Bluff and 150 juvenile salmon from Dibble and Blue Tent creeks, 2 intermittent tributaries that enter the Sacramento River immediately upstream from Red Bluff. Although Ganssle (1966), Sasaki (1966), Kjelson et al. (1982), and others documented the gut contents of juvenile salmon from the Sacramento-San Joaquin Delta and San Francisco Bay, the forage base in this estuarine habitat can differ considerably from that upstream in the Sacramento River. The purpose of our study was to supplement existing information on forage taxa consumed by juvenile salmon in the upper Sacramento River by documenting their gut contents.

In March and May 1998, sampling sites were established along the upper Sacramento River as follows (from upstream to downstream) (Fig. 1): adjacent to Jellys Ferry Road (Jellys Ferry; N40°20'54.1", W122°10'55.0"); at Red Bluff Lake

[1] Saiki, M.K. 2000. Assessment of copper, cadmium, and zinc contamination in juvenile chinook salmon and selected fish-forage organisms (aquatic insects) in the upper Sacramento River, California. Final report prepared for U.S. Fish and Wildlife Service, Sacramento Fish and Wildlife Office, Sacramento, California, USA.

[2] Schaffter, R.G., P.A. Jones, and J.G. Karlton. 1983. Sacramento River and tributaries bank protection and erosion control investigation – evaluation of impacts on fisheries: Final report. California Department of Fish and Game, Bay-Delta Fishery Project, Stockton, California, USA.

[3] Moore, T.L. 1997. Condition and feeding of juvenile chinook salmon in selected intermittent tributaries of the upper Sacramento River. MS Thesis, California State University, Chico, California, USA.

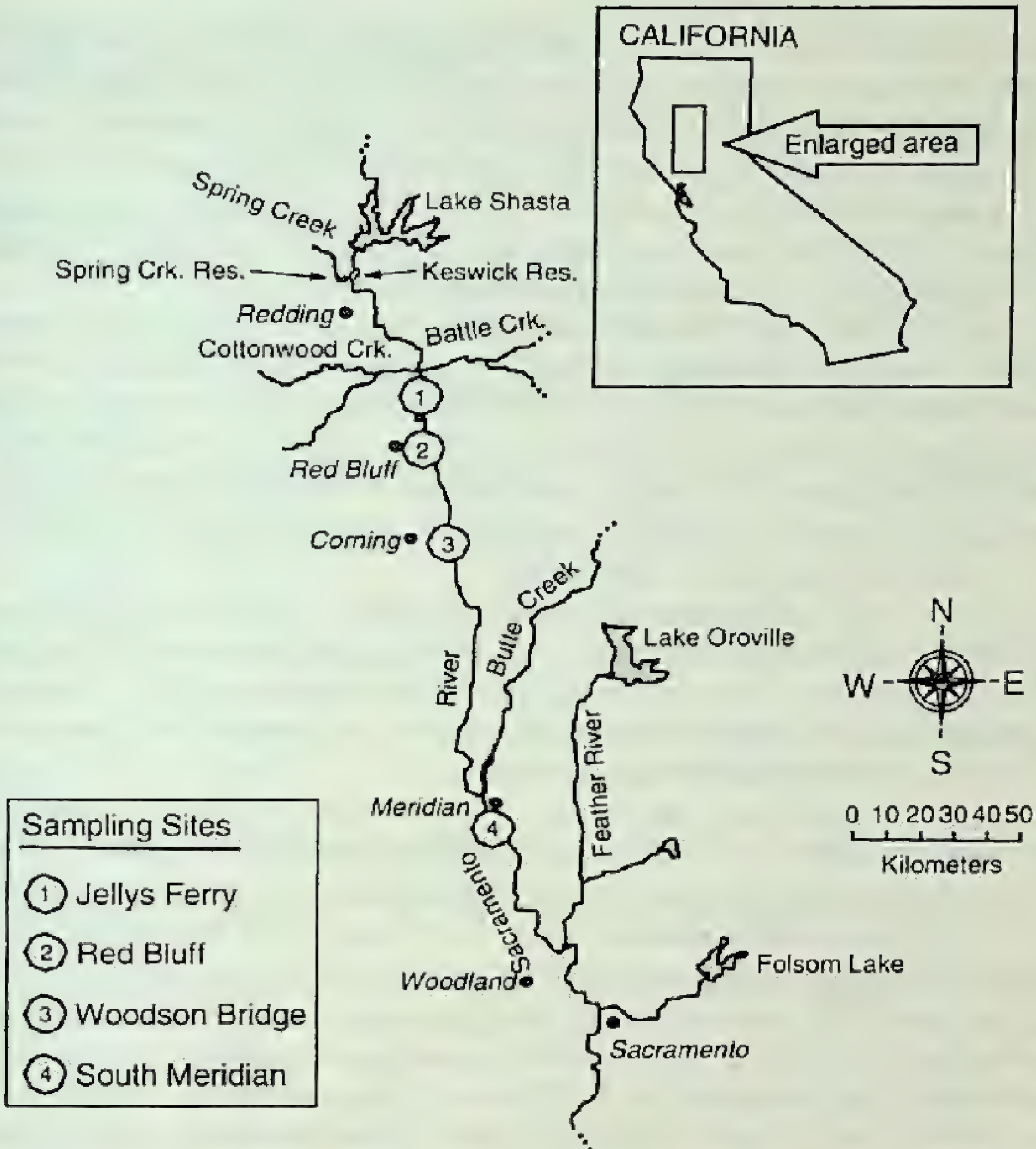

Figure 1. Map of the study area with locations of sampling sites on the upper Sacramento River.

(Red Bluff; N40°09'19.0", W122°12'23.6"); near the City of Corning (Woodson Bridge; N39°54'31.9", W122°05'29.0"); and below the City of Meridian (South Meridian; N39°06'47.2", W121°54'12.2"). Juvenile chinook salmon were captured from these sites with beach seines (3.2-mm bar mesh). Fish were measured to the nearest millimeter standard length (SL), weighed to the nearest 0.01 g, coded with unique identification numbers, and preserved in 10% formalin. About 4 days later, the fish were transferred into 70% isopropyl alcohol and stored until gut analysis could be performed. Although fin-clipped chinook salmon were excluded from our study, some fish may have originated from the Coleman National Fish Hatchery because, of approximately 12 million salmon released into Battle Creek during March–April 1998, only 1 million fish were fin clipped. However, studies elsewhere have found that hatchery salmonids adapt to wild prey as rapidly as 1 week after release (Johnsen and Ugedal 1986, Reirz et al. 1998), so potential inclusion of some hatchery chinook salmon in our sample should not bias results.

Stomach contents from the anterior end of the esophagus to the pyloric sphincter were identified to the lowest taxonomic level possible using standard keys (Usinger 1971, Merritt and Cummins1978, Pennak 1978). Damp-dry biomass (nearest 0.00001 g) of each taxonomic category was recorded for individual fish. Percent damp-dry biomass of each taxon consumed by fish from a given site was calculated as 100 times the sum of the biomass of that taxon for all fish from the site divided by the sum of the biomass of all taxa for all fish from the site.

A total of 114 juvenile chinook salmon averaging 56±9 mm SL (weight, 2.78±1.11 g; values are arithmetic mean±SD) was collected during this study: 25 came from Jellys Ferry (all in May), 26 from Red Bluff (all in March), 36 from Woodson Bridge (11 in March, 25 in May), and 27 from South Meridian (2 in March, 25 in May). Judging from daily fork length criteria for 4 runs of juvenile salmon in the Sacramento River (Fisher[4] 1992, as modified by Greene[5] 1992), fish used in our study were most likely progeny of fall-run adults.

Gut contents of juvenile chinook salmon captured in March and May were combined after preliminary comparisons of mean damp-dry biomasses of the forage taxa ingested by fish from Woodson Bridge and South Meridian yielded overlapping 95% confidence intervals. Only 2 fish from Red Bluff, 1 fish from Woodson Bridge, and 1 fish from South Meridian had empty guts.

On average, the most important forage of juvenile chinook salmon were midge (Diptera: Chironomidae) larvae and pupae, caddisfly (Trichoptera: Hydropsychidae) larvae, and amorphous organic matter (mostly unidentifiable insect remains) (Table 1). At Jellys Ferry, gut contents consisted mostly of midge larvae and pupae (77.2%) and Cladocera (12.1%), whereas at Red Bluff, amorphous organic matter (25.9%), hydropsychid caddisfly larvae (21.1%), and Hemiptera (11.4%) were the most important forage taxa. At both Woodson Bridge and South Meridian, juvenile salmon consumed mostly hydropsychid caddisfly larvae (Woodson Bridge, 25.5%; South Meridian, 34.5%) and amorphous organic matter (Woodson Bridge, 22.9%; South Meridian, 16.5%). Midge larvae and pupae (15.9%) were also important at Woodson Bridge, whereas mayfly (Ephemeroptera: Baetidae) nymphs (13.5%) were important at South Meridian. Other taxa contributed <10% of overall damp-dry biomass of gut contents.

Although many studies are available on the food habits of juvenile chinook salmon in fresh waters of the Pacific Northwest, including northern California and Alaska (e.g., Loftus and Lenon 1977, Busby and Barnhart 1995, Muir and Coley 1996), and elsewhere in the world (e.g., Johnson 1981, Field-Dodgson 1988, Sagar and Glova 1988, Rutledge and Power 1992, Smirnov et al. 1994), few studies have occurred in the upper Sacramento River drainage. According to an early report by Rutter (1904),

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[4] Fisher, F.W. 1992. Chinook salmon *Oncorhynchus tshawytscha* growth and occurrence in the Sacramento-San Joaquin River system. California Department of Fish and Game, Inland Fisheries Division, Red Bluff, California, USA.

[5] Greene, S. 1992. Estimated winter-run chinook salmon salvage at the State Water Project and Central Valley Project delta pumping facilities. Memorandum to R. Brown, 5/8/92. California Department of Water Resources, Sacramento, California, USA.

Table 1. Damp-dry biomass of gut contents from 114 juvenile chinook salmon at 4 sites on the upper Sacramento River, spring 1998.

	Jellys Ferry (n = 25)		Red Bluff (n = 26)		Woodson Bridge n = 36)		South Meridian (n = 27)	
Taxonomic category	Grams	%	Grams	%	Grams	%	Grams	%
Coleoptera:								
Larvae	0.00040	0.09	0.01770	6.16	0.00670	2.39	0.01310	4.44
Adult	0.00080	0.18	0.02590	9.01	0.02530	9.02	0.00320	1.08
Diptera:								
Chironomidae Larvae and pupae	0.34791	77.20	0.00890	3.10	0.04460	15.90	0.02522	8.55
Other Diptera Larvae and pupae	0.00350	0.78	0.00390	1.36	0.01560	5.56	0.01860	6.30
Diptera adults	0.00130	0.29	0.01310	4.56	0.00290	1.03	0.00060	0.20
Ephemeroptera:								
Baetidae nymphs	0.00330	0.73	0.00490	1.71	0.01370	4.88	0.03970	13.45
Other mayfly nymphs	0.00001	<0.01	0.00000	0.00	0.00000	0.00	0.00000	0.00
Mayfly adults	0.00000	0.00	0.00000	0.00	0.00210	0.75	0.00000	0.00
Hemiptera	0.00090	0.20	0.03260	11.35	0.01230	4.38	0.01410	4.78
Trichoptera:								
Hydropsychidae larvae	0.01580	3.51	0.06050	21.06	0.07160	25.53	0.10180	34.50
Other caddisfly larvae	0.00082	0.18	0.00220	0.76	0.00040	0.14	0.00000	0.00
Caddisfly adults	0.00000	0.00	0.00000	0.00	0.00000	0.00	0.00370	1.25
Other insects	0.01700	3.77	0.02130	7.41	0.01520	5.42	0.01240	4.20
Cladocera	0.05460	12.12	0.00000	0.00	0.00000	0.00	0.00000	0.00
Other invertebrates	0.00060	0.13	0.01200	4.18	0.00590	2.10	0.01270	4.31
Amorphous matter	0.00370	0.82	0.07440	25.90	0.06420	22.89	0.04860	16.47
Sand	0.00000	0.00	0.00990	3.45	0.00000	0.00	0.00140	0.47
Total	0.45064	100.00	0.28730	100.00	0.28050	100.00	0.29512	100.00

juvenile chinook salmon in the Sacramento River and its tributaries between Redding and Grimes (the approximate longitudinal extent of our study area) consumed mostly adult or terrestrial insects and immature stages of aquatic insects. Included among the insect taxa were Odonata, Ephemeroptera, Plecoptera, Orthoptera, Hemiptera, Trichoptera, Lepidoptera, Coleoptera, Diptera (including midges), and Hymenoptera. More recently, Schaffter et al.[2] (1983) found that juvenile chinook salmon captured from the river between Red Bluff and Chico fed primarily on midges, baetid mayflies, and Aphididae. In August 1990, identifiable gut contents of 29 juvenile chinook salmon from Lake Redding on the upper Sacramento River consisted mostly of Cladocera and midge larvae (M.K. Saiki, unpublished data). Juvenile chinook salmon from the lower American River consumed all life stages of midges, nymphs, and adults of baetid mayflies and larvae of hydropsychid caddisflies (Merz and Vanicek

1996). Finally, Moore[3] (1997) reported that juvenile salmon in the Sacramento River at Red Bluff fed mostly on midges, baetid and ephemerellid mayflies, hydropsychid caddisflies, and perlodid stoneflies, whereas juvenile salmon in Dibble and Blue Tent creeks fed mostly on midges, baetid mayflies, capniid stoneflies, and larval fish. These observations are generally consistent with findings from our study, which showed that gut contents of juvenile salmon were composed mostly of immature aquatic insects – especially midge larvae and pupae and hydropsychid caddisfly larvae – and amorphous organic matter.

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